INHERITANCE STUDIES IN PISUM. V. THE INHERITANCE OF SCIMITAR POD[1]

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INTRODUCTION

Certain varieties of field peas, *Pisum arvense* L., or *P. sativum* var. *arvense* of some authors, are characterized by a long, comparatively narrow, string-bean-shaped pod, curved in varying degrees in scimitar fashion, and terminating in an acute apex. These varieties vary in both length and width of pod, but in each case the dimensions show the same proportional relation to each other, so that although a variety may have very small pods, the length-width relation gives a long, narrow, string-bean-shaped pod. The experimental work reported in succeeding pages records the results of crossing a variety with the scimitar character with six varieties of peas characterized by broad, straight pods, and 2 varieties with broad pods, very slightly curved. These experiments involve a total of over 2290 F_1, F_2, F_3 and F_4 plants.

[1] BROOKLYN BOTANIC GARDEN Contributions No. 43. These studies on the genetics of Pisum were carried on in collaboration with the Office of Forage Crop Investigations and the Office of Horticultural and Pomological Investigations, U. S. DEPARTMENT OF AGRICULTURE.

THE TYPES USED

The varieties used, together with the source from which they were obtained and the numbers by which they are designated in my records are listed in table 1.

TABLE 1

List of varieties used, with source and pedigree number.

PEDIGREE NUMBER	VARIETY	SOURCE
5	Homozygous segregate from Chinese native×Mummy	A. D. DARBISHIRE
32	Wachs Schwert	HAAGE and SCHMIDT 1302*
38	Acacia	W. BATESON
70	Juno	PETER HENDERSON SEED CO.
81	Nero	HAAGE and SCHMIDT 1330
82	Mammut	HAAGE and SCHMIDT 1296
87	Graue Riesen Schnabel	HAAGE and SCHMIDT 1290
157	Brown Abyssinian	U.S. DEPT. AGRIC. S.P.I. 25680†
190	Desipisum	U.S. DEPT. AGRIC. S.P.I. 21289

* Number designations in 1915 catalog.
† Office of Seed and Plant Introduction.

Table 2 gives a crude measure of the pod-dimension characters of each variety, accurate enough for the present study. The pods were measured in both the green mature and dry mature states. The pods of each plant of a given variety vary within the ranges indicated, the smaller pods representing the end of the bearing season. Numbers 32 and 82 had non-parchmented pods, hence the green-pod dimensions give a more accurate concept of their relative length-width dimensions, as they

TABLE 2

Pod width and length in the varieties used.

PEDIGREE NUMBER	RANGE OF WIDTH PER PLANT IN CENTIMETERS		RANGE OF POD LENGTH PER PLANT IN CENTIMETERS	
	Green	Dry	Green	Dry
5	———	1.3–1.5	———	4.0– 6.0
32	1.5–2.0	1.3–1.7 (mode 1.4)	6.0– 9.0	3.5– 9.0 (mode 8.0)
38	.....	1.2–1.5	.....	4.0– 6.5
70	.....	1.5–1.8	.....	7.7– 8.5
81	1.5–1.8	1.5–1.8	4.5– 6.5	4.0– 7.0
82	2.0–2.6	1.7–2.2 (mode 2.0)	6.5–12.5	5.7–12.5
87	1.2–1.4	1.1–1.4 (mode 1.1)	6.0–10.0	6.0–10.0
157	.....	1.2–1.3	.....	4.0– 4.5
190	.....	0.8–1.0	.....	3.5– 4.5

shrink considerably on maturing, while shrinkage is relatively slight in the parchmented types.

EXPERIMENTAL WORK

The behavior of the parent strains

All the varieties used were inbred for two years or more and doubtless had been inbred for a large number of generations, since the flowers of nearly all varieties known to me are nearly always self-pollinated in the bud stage before the flowers open. The literature on cross-pollination in peas is summarized in a previous publication (WHITE 1917), together with

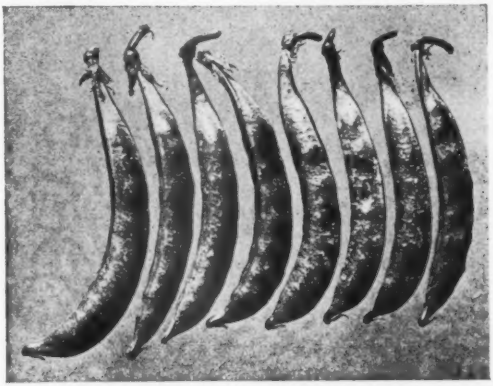


FIGURE 1.—Random sample of pods, one from a single plant, showing the narrow scimitar shape of the pods of the variety Graue Riesen Schnabel (87).

data on cross-pollination in field cultures at the BROOKLYN BOTANIC GARDEN. Numbers 38, 70, 81, 82, 157 and 190 bred true for straight broad pods. The pods of number 82, as can be seen from table 2, are greatest in both length and breadth, while those of number 190 are smallest in these dimensions. From a width-length standpoint, all these types are to be classed as broad-podded. Numbers 5 and 32 bred true to broad-poddedness, but are slightly curved, though this curvature is so slight in most cases as to be easily distinguished from that of number 87. Number 87 bred true to the narrow, sickle-curved pod character previously described, which I have called "scimitar." Environmental differences, such as are ordinarily encountered in field and greenhouse cultures, did not effect particularly noticeable changes in the pod characters under discussion. When the pods were decreased in size through poor soil, unfavorable weather, etc., the two types of pods retained their

differences. Figure 1 is a random sample of pods, one from each plant, typical of the variety number 87. Figure 2 shows a similar sample of pods, one from each plant, of the broad straight-pod type, as found in number 38.

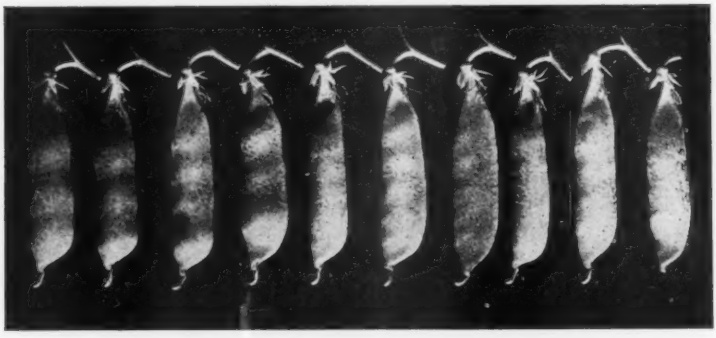


FIGURE 2.—Random sample of pods, one from a single plant, showing the broad, straight-pod type as illustrated by the variety Acacia (38).

The behavior of the crosses

Wachs Schwert (32) × Graue Riesen Schnabel (87)

Four F_1-generation plants of this cross were grown, giving rise to 4 F_2-generation families, totaling 55 plants. A summary of the F_1 and F_2 results is given in table 3. The ranges of the pod widths are in parenthesis.

TABLE 3

F_1 and F_2 data from crossing a variety with broad, slightly curved pods (32) with a variety with narrow, scimitar pods (87).

GENERATION AND PEDIGREE NUMBER	NUMBER OF PLANTS	CHARACTER OF PODS	
		Broad, slightly curved	Narrow, scimitar
F_1	4	4(1.7-2.0 cm wide)	0
F_2-1	14	9(1.9-2.2 cm)	5(1.2-1.5 cm)
F_2-2	15	9(1.9-2.2 cm)	6(1.0-1.4 cm)
F_2-3	13	11(1.5-2.0 cm)	2(0.7-1.3 cm)
F_2-4	13	11(1.8-2.1 cm)	2(1.2-1.3 cm)
Total F_2	55	40	15
Expected (3:1)	*55*	*41.25*	*13.75*

Forty-three of the 55 F_2 plants gave rise to 43 F_3 families, totaling 385 plants, each family consisting in the great majority of cases of from 5 to 15 or more plants. In a few cases, the family consisted of only 3 or 4 individuals, but these were families derived from the scimitar segregates and consisted wholly of scimitars. Thirty-three of the 43 F_2 plants tested by their F_3 progeny were broad-pod, the remaining 10 being scimitar. Fifteen of the broad-pod F_2 plants gave only broad-pod F_3 progeny, while 18 broad-pod F_2 plants were heterozygous, giving both broad-pod and scimitar segregates in F_3. The total number of plants in the F_3 heterozygous families was 153, divided into 102 broad-pod : 51 scimitar. This is exactly a 2:1 ratio, whereas the theoretically expected ratio, as judged by the F_2 results, should approximate 3:1. The F_3 generation was field grown and many of the plants died from disease before reaching the pod-bearing stage, whereas the F_2 generation was greenhouse grown and gave 100 percent germination and 100 percent plants reaching maturity.

Acacia (38) × Graue Riesen Schnabel (87)

The F_1- and F_2-generation data on this cross are given in table 4. The range of pod width is in parenthesis.

TABLE 4

F_1 and F_2 data from crossing a broad straight-pod variety (38) with the narrow, scimitar-pod variety (87).

GENERATION AND PEDIGREE NUMBER	NUMBER OF PLANTS	CHARACTER OF PODS	
		Broad straight	Narrow scimitar
F_1	2	2 (1.8 cm)	
F_2-1	30	27 (1.2-2.0)	3 (1.2-1.3)
F_2-2	29	18 (1.3-2.1)	10+1? (1.2-1.6)
Total F_2	59	45	13+1?
Expected (3:1)	*59*	*44.25*	*14.75*

In F_3 6 F_2 broad, straight-pod segregates gave 4 families homozygous for broad straight pods and 2 heterozygous families, while 3 F_2 scimitar segregates in F_3 bred true to scimitar. Figure 3 shows 5 pods from 5 different F_3 plants of a heterozygous family, the first of which, beginning at the left, illustrates the type of pods on heterozygous plants. Pods 2 and 3 show the character of pods on the segregates homozygous for broad straight pods. Pods 4 and 5 are pods from F_3 segregate scimitar plants. The character of the pods of the pure broad straight-pod parent (number 38) is shown in figure 2.

Juno (70) × Graue Riesen Schnabel (87)

Table 5 gives the F_1- and F_2-generation results of this cross. No data were taken on the range of pod diameters, since the difference between the parents in this respect made the F_2 classification relatively simple.

FIGURE 3.—A single pod from each of 5 F_3 plants of a heterozygous family of No. 38×No. 87, showing the segregate types S_sS_s, S_sS_s and s_ss_s.

TABLE 5

F_1 and F_2 data from crossing a broad straight-pod variety (70) with the narrow, scimitar-pod type (87).

GENERATION AND PEDIGREE NUMBER	NUMBER OF PLANTS	CHARACTER OF PODS	
		Broad straight	Narrow scimitar
F_1	4	4 (1.8-2.0 cm)	.....
F_2-1	12	10	2
F_2-2	15	12	3
F_2-3	35	28	7
F_2-4	29	22+1?	6
Total F_2	91	72+1?	18
Expected (3:1)	*91*	*68.25*	*22.75*

Eight F_2 broad-pod segregates when tested in F_3 showed that 6 were heterozygous and 2 homozygous. The 6 heterozygotes gave a ratio of 62 : 23, the theoretically expected being 63.75 broad-pod straight: 21.25 narrow scimitar. Four F_2 scimitars gave all scimitar progeny in F_3. Figure 4 shows the segregation of pod types (broad straight and scimitar)

in a heterozygous F_3 family of this cross. Fifteen segregate plants are represented, one typical pod from each. Beginning at the left, the first 9 illustrate the homozygous broad straight pod and the heterozygous types,

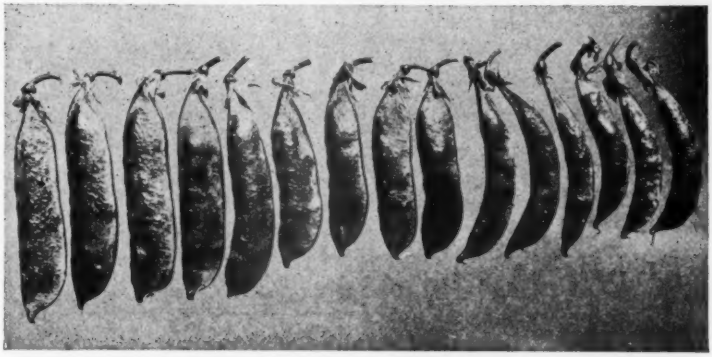


FIGURE 4.—One pod from each of 15 plants of an F_3 heterozygous family (No. 70×No. 87), showing segregation of broad straight or slightly curved (the first 9) and narrow scimitar (the last 6).

while the remaining six pods are from 6 scimitar F_3 segregates. Figure 5 shows pods from 10 F_3 plants derived from an F_2 scimitar segregate. All are uniformly scimitar. For illustration of the scimitar parent, see figure 1.

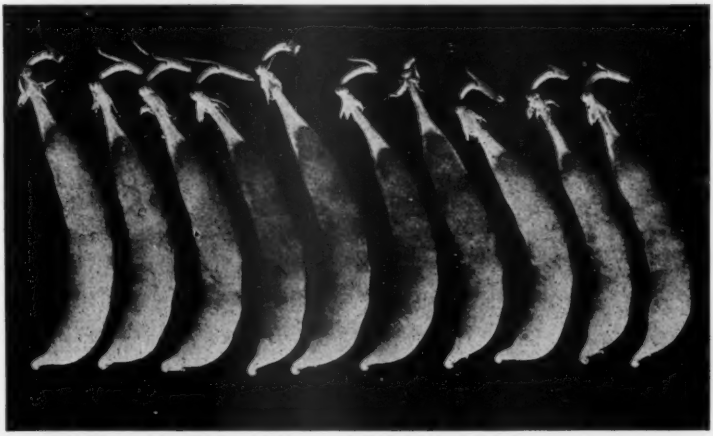


FIGURE 5.—A single pod from each of 10 plants of an F_3 family (No. 70×No. 87) homozygous for scimitar.

Nero (81) × Graue Riesen Schnabel (87)

Four F_1 plants of this cross were grown, and all had broad straight pods averaging 1.8 cm in diameter. Table 6 gives the data for the 4 F_2 families.

TABLE 6

F_2 data from broad straight pod (81) × narrow scimitar pod (87).

PEDIGREE NUMBER	NUMBER OF PLANTS	CHARACTER OF PODS	
		Broad straight	Narrow scimitar
F_2-1	23	19	4
F_2-2	11	9	2
F_2-3	14	8	6
F_2-4	17	15	2
Total	65	51	14
Expected (3:1)	*65*	*48.75*	*16.25*

Forty-five F_3 families were grown, thirty-five of which were derived from F_2 broad, straight-pod segregates and ten from F_2 scimitar parents. Ten of the F_2 broad-pod segregates bred true, giving only F_3 progeny with broad, straight pods, while 25 F_2 broad-pod segregates were heterozygous, giving a total ratio of 135 broad straight-pod : 59 scimitar, the theoretically expected ratio being 145.5 : 48.5.

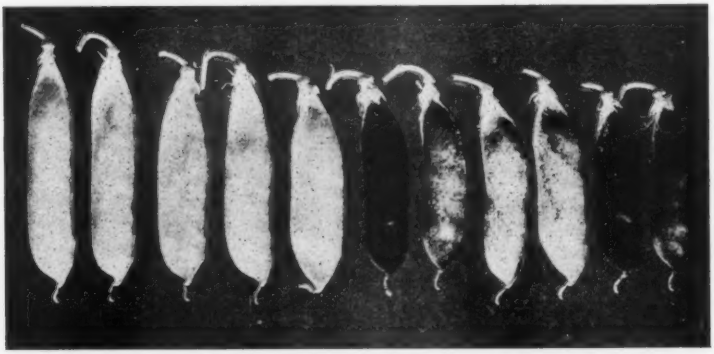


FIGURE 6.—Eleven pods from 11 plants of Nero (81), a broad straight-pod type.

One F_3 heterozygous family was excluded from the above calculations because of a peculiar ratio of 1 broad : 6 scimitar. Twelve seeds were planted, only 7 maturing, and this may explain the ratio, as scimitars in general are more disease-resistant under field conditions. On the other hand, the F_2 may have been wrongly classified as well as the 1 F_3. Figure

6 illustrates the character of the pods from the straight broad-pod type (number 81).

Graue Riesen Schnabel (87) × segregate (5)

Five F_1 plants of this cross were grown and all had broad, slightly curved pods such as the parent type (5) had. The range of pod diameter was 1.6 to 1.8 cm. The F_2 data from the progeny of these F_1's are given in table 7, with the pod widths in parenthesis.

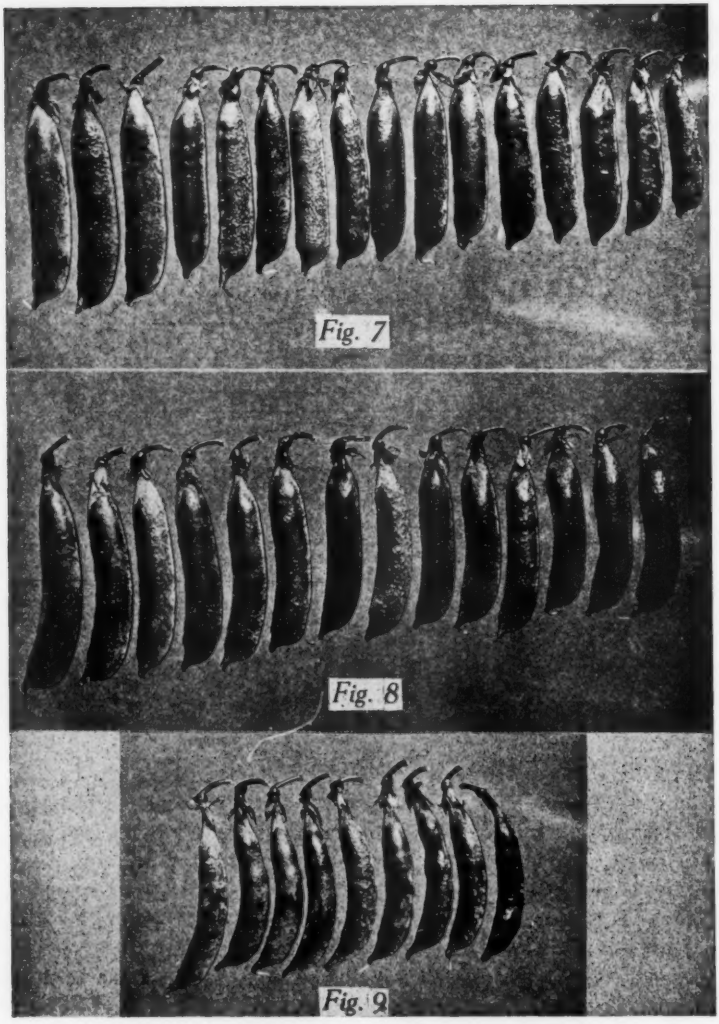
TABLE 7

F_2 data from scimitar (87) × broad-pod type (5).

PEDIGREE NUMBER	NUMBER OF PLANTS	CHARACTER OF PODS	
		Broad straight or very slightly curved (5) type	Narrow scimitar (87) type
F_2-1	18	14 (1.2-1.8 cm)	4 (1.0-1.2)
F_2-2	28	18 (1.2-1.9 cm)	10 (1.0-1.4)
F_2-3	11	8 (1.5-2.2 cm)	3 (1.2)
F_2-4	17	13 (1.3-2.0 cm)	4 (1.1-1.2)
F_2-5	22	18 (1.2-2.0 cm)	4 (1.1-1.4)
Total	96	71	25
Expected (3:1)	*96*	*72*	*24*

Figure 1 shows the pod character of the scimitar parent (87) while figures 7, 8 and 9, although photographed from F_3-generation progeny, illustrate the character of the F_2 segregate pods. The broad-pod segregates were of 2 types, straight broad or slightly curved and broad, like the pods of the pollen parent (number 5), illustrated by figure 10. F_1 heterozygotes in all these crosses of straight or slightly curved broad-pod types with the narrow scimitar type, are very slightly curved, but this difference is often so slight that separate classification is difficult, so they are grouped with the homozygous broad pods.

Thirty F_3 families of this cross were grown, 17 from F_2 broad-pod segregates and 13 from F_2 scimitar segregates. The latter bred true, giving only F_3 families of scimitar-pod plants. Three of the broad-pod F_2 segregates were homozygous, giving only broad-pod plants in F_3, while 14 such F_2 plants were heterozygous and gave F_3 families with a combined total ratio of 283 broad : 89 scimitar, the theoretically expected ratio, on the assumption of a one-factor difference, being 279 broad : 93 scimitar.



FIGURES 7, 8 and 9.—The pod character of the three different classes of segregates in one heterozygous family (No. 87×No. 5)-4-8. Each plant is represented by one pod. The classes are: broad straight (figure 7), broad slightly curved (figure 8) and scimitar (figure 9). The broad straight class illustrated here evidently involves other factors, but contains the allelomorph of scimitar.

Graue Riesen Schnabel (87) × Mammut (82)

Seven F_1 plants of this cross were grown and all had broad slightly curved pods, ranging from 1.7 to 2.5 cm in width. The F_2 data are presented in table 8, with range of pod width in parenthesis.

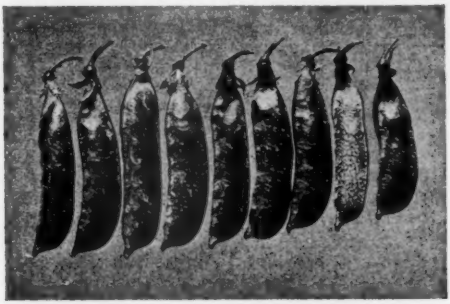


FIGURE 10.—Nine pods from 9 plants of the variety designated "segregate (5)," showing the broad, slightly curved pod character.

TABLE 8

F_2 data from narrow, scimitar-pod type (87) × broad-pod type (82).

PEDIGREE NUMBER	NUMBER OF PLANTS	CHARACTER OF PODS	
		Broad, slightly curved (82) type	Narrow scimitar (87) type
F_2-1	16	11 (2.0-2.4 cm)	5 (1.2-1.5)
F_2-3	23	19 (1.8-2.4 cm)	4 (1.3-1.5)
F_2-1a	5	3 (2.0-2.4 cm)	2 (1.3-1.4)
F_2-2a	12	11 (1.8-2.4 cm)	1 (1.4)
F_2-3a	13	8 (2.0-2.5 cm)	5
F_2-4a	11	8 (1.7-2.5 cm)	3 (1.2-1.3)
Total	80	60	20
Expected (3:1)	*80*	*60*	*20*

Nine F_3 families were grown. Three of these were of F_2 scimitar parentage and bred true in F_3, while 6 were derived from F_2 broad-pod segregates. Three of the families were all broad-pod, while 3 of them were heterozygous and when combined had 24 broad-pod : 9 scimitar, the expected on a 3 : 1 basis being 24.75 : 8.25.

Brown Abyssinian (157) × Graue Riesen Schnabel (87)

The 3 F_1 plants were broad-pod, straight, with a pod width of 1.5 to

1.7c m. Table 9 gives the F_2 data with the pod widths in parenthesis. No F_3 generation was grown.

TABLE 9

F_2 data from a straight broad-pod type (157) × a narrow, scimitar type (87).

PEDIGREE NUMBER	NUMBER OF PLANTS	CHARACTER OF PODS	
		Broad straight	Narrow scimitar
1	10	7 (1.2-1.6 cm)	3 (1.0-1.2)
2	5	4 (1.3-1.8 cm)	1 (1.2)
3	7	7 (1.3-1.8 cm)	0
Total	22	18	4
Expected (3:1)	*22*	*16.5*	*5.5*

Desipisum (190) × Graue Riesen Schnabel (87)

The 4 F_1 plants of this cross had slightly curved, broad pods (from a length-breadth standpoint) with a range in width from 1.2 to 1.5 cm. Only 1 F_2 family of 15 plants was grown, these giving a ratio of 10 broad-pod (0.9 to 1.5 cm) : 5 scimitar (0.9 to 1.1 cm). Two of the F_2 scimitars gave in F_3 all scimitar progeny (22 plants).

COMBINED RESULTS

In the preceding pages, detailed data on the F_1, F_2 and F_3 generations together with their parents have been presented. Eight series of crosses were made, each one involving, as one parent, the field-pea variety, Graue Riesen Schnabel (87) with narrow scimitar-shaped pods, and as the other parent, any one of eight different pea varieties, each of which bred true to broad straight or to broad, slightly curved pods.

The F_1 generation in each cross had slightly curved, broad pods, so that the ordinary or wild type is not absolutely dominant, though almost so. Reciprocal crosses gave the same results. Altogether, 33 F_1 plants were grown.

The F_2 generation data are summarized in table 10. In all but a very few individuals, no difficulty was experienced in separating and properly classifying the segregates. In these few cases, the difficulty was due not to the pod diameter, but to the extent of pod curvature. In these exceptional cases, the pods were not curved as much as in the majority of the F_2 scimitar segregates.

A total of 105 F_2 segregates with broad, straight or slightly curved pods, representing six of the crosses, were used as parents of F_3 families. From these, the ratio of F_3 homozygous to heterozygous families was 37 : 68, the theoretical expectancy on a 3 : 1 basis being 35 : 70. The 68 F_3 hetero-

zygous families gave a ratio of 606 broad, straight or slightly curved : 231 narrow scimitar, the theoretical expectancy being 627.75 : 209.25.

TABLE 10

Summary of F_2 data from crosses involving broad straight or broad slightly curved pods and scimitar pods.

PEDIGREE NUMBER	NUMBER OF PLANTS	CHARACTER OF PODS	
		Broad straight or slightly curved	Narrow scimitar
32×87	55	40	15
38×87	59	45	13+1?
70×87	91	72+1?	18
81×87	65	51	14
87×5	96	71	25
87×82	80	60	20
157×87	22	18	4
190×87	15	10	5
Total	483	367+1?	114+1?
Expected (3:1)	*483*	*362.25*	*120.75*

Forty-five F_2 scimitar segregates, when tested by their F_3 progeny, bred true to scimitar. Combining the F_2 and F_3 data from heterozygous families gives a total of 1320 plants, in the ratio of 973+1? broad-pod: 345+1? scimitar, 990 broad-pod : 330 being the theoretical expectancy on a 3:1 basis.

DISCUSSION AND INTERPRETATION

The facts as described in previous pages are most simply interpreted on the basis of a one-factor difference between the varieties with broad, straight, or broad, slightly curved pods and the scimitar-pod type, Graue Riesen Schnabel (number 87). Designating this factor as S_s, the variety Graue Riesen Schnabel is $s_s s_s$, while the broad-pod varieties each are $S_s S_s$ in respect to the allelomorph of scimitar, since the broad-pod character in the sense in which it has been used here, most nearly approaches the character of the pods of the wild-pea types. The nomenclature followed is in accordance with the suggestions of the Committee on Genetic Form and Nomenclature of the AMERICAN SOCIETY OF NATURALISTS (LITTLE 1921). The F_1 plants have the formula $S_s s_s$, while the F_2 consists of 2 visibly different classes—broad-pod and scimitar, since the heterozygous class could not be accurately differentiated from the homozygous broad-pod segregates. These two classes occur in a ratio of 3 broad-pod : 1 scimitar and are easily differentiated. The F_3 generation gives the results

expected on a monohybrid interpretation. The recessive scimitars breed true, while the F_2 broad-pod segregates give F_3 homozygous and heterozygous families in a ratio approximating 1 : 2.

There is no intention to imply here that only one pair of factors is involved in determining the inheritance of pod shape and width in the crosses described. As the data in table 2 show, between the various broad-pod varieties used there is a wide diversity in pod diameters characteristic of each type, and these divergencies are doubtless due to other factorial differences. Each of the broad-pod varieties used, however, carries the S_s allelomorph of scimitar. The scimitar type, so far as I know, represents the extreme divergence in this direction, from the wild type.

SUMMARY

1. The F_1-, F_2- and F_3-generation results of crosses between 8 different varieties of peas, breeding true to broad, straight, or broad slightly curved pods, and a single variety, Graue Riesen Schnabel, with narrow scimitar-curved pods, are described in detail, as respects the inheritance of the scimitar character.

2. In F_1 the broad-pod character is nearly dominant. In F_2, 2 segregate classes are easily distinguishable,—broad, straight, or broad, slightly curved-pod types and narrow scimitar-pod types,—in a ratio approximating 3 : 1. The F_3-generation data give the usually expected results where a monohybrid F_2 ratio is involved.

3. The gene for scimitar is designated s_s, while its normal allelomorph broad-pod, etc., is S_s.

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MUTANT RACES DERIVED FROM *OENOTHERA LAMARCKIANA SEMIGIGAS*

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INTRODUCTION

The progeny of *Oenothera Lamarckiana semigigas* splits up into numerous mutant types, among which the prominent ones are seen to repeat the external features of the old mutated races of *Oe. Lamarckiana* more or less clearly. Besides these, deviating types are observed, but as a rule the deviations are small and do not constitute really new characters. They are to be considered as the result of different combinations of the same elementary changes.

The question arises, whether these mutants are also like the older races in their hereditary characters. If this is so, they may be considered as belonging to the same general types and as identical with them in the special cases. The *semigigas* would then have to be considered simply as due to a sevenfold mutation or to the simultaneous production of the seven main derivatives lately distinguished by BOEDIJN and myself for *Oe. Lamarckiana*, and of their secondary forms (DE VRIES and BOEDIJN 1923).

This problem could be solved by means of the cultivation of the second generation of the mutants described in previous articles. These were derived from three crosses, made in 1922, on a biennial specimen of *Oe.* (*lata*×*Lamarckiana*) *semigigas*. For one of these the pollen of *Oe.* (*biennis*×*Lamarckiana*) *velutina* was used and for the offspring of this

cross the external features of each type have been described and the chromosomes counted for every individual by BOEDIJN and myself (1924 a, b, p. 258). For the two others I have chosen the pollen of *Oe. Lamarckiana* mut. *tardescens* and of *Oe. Lamarckiana* mut. *blandina*. *Tardescens* has pure *velutina* pollen and the offspring behave like those of the first-named cross. In the pollen of *Oe. blandina* (synonym: *Oe. Lamarckiana* mut. *velutina*) the characteristic lethal factor of the *velutina* type is absent, and therefore the corresponding seeds, which are ordinarily barren, are viable here, producing a large part of the progeny in consequence of their preferential fertilization (DE VRIES 1924 a). For these two crosses the chromosomes of the mutants have not been counted, and they are grouped in the following tables according to their external marks and to the condition of their offspring.

After self-fertilization in 1923 some of the mutants of *Oe. semigigas* produced a sufficient supply of seeds, while others gave only a small harvest. Only the first category could be used for the present purpose, and cultures of about 60 individuals were derived from them, wherever possible, in 1924. Almost all of these plants have flowered, with the exception of a small part of specimens of the *Lamarckiana* type, when this was indubitably clear in the stage of rosettes of root leaves.

The different constituents of the cultures have been counted in this stage and afterwards during the summer, especially shortly before flowering and in the flowering and fruiting condition. The general results of these separate countings will be given in the tables. These deal with representative members of five of the seven main classes and with some of their secondary forms. In the categories of *lata* and *pallescens* no plants have given a useful amount of seeds, but the tables may suffice to warrant the general conclusions.

Oenothera Lamarckiana semigigas MUT. *scintillans*

From the cross of *Oe. semigigas* with *Oe.* (*biennis*×*Lamarckiana*) *velutina* studied by BOEDIJN and myself (1924 b, p. 261) I had two, and from that with *Oe. tardescens*, three plants of *Oe. scintillans* (1924 b, p. 224), all of them of a very pure type. They proved to be sufficiently fertile after self-fertilization and about sixty specimens of the offspring of each were cultivated and counted during the flowering period. The two first-named parent plants had 15 chromosomes, but for the three others the number has not been determined. The cultures showed exactly the same splitting as is known for the old race of *Oe. Lamarckiana* mut. *scintillans*. The main types were *scintillans*, *Lamarckiana* and *oblonga*.

Moreover, there were barren seeds which amounted to 34 percent in the first culture, and a small number of mutants.

The countings on the beds are given in table 1. No. 1 and No. 2 were derived from the cross with *velutina*, Nos. 3 to 5 from that with *tardescens*.

TABLE 1

Oenothera semigigas mut. scintillans. Second generation.

Scintillans PARENT	TOTAL	*Lamarckiana*	*Scintillians*	*Oblonga*	MUTANTS
No. 1	58	52	2	3	1
No. 2	38	32	2	4	0
No. 3	60	48	4	7	1
No. 4	60	41	7	9	3
No. 5	60	51	4	3	2
Total	276	224	19	26	7
Percentage		81	7	9	3

For my race of the same name the figures are, in the main, 70 percent *Lamarckiana*, 18 percent *scintillans*, 10.5 percent *oblonga* and 1.5 percent mutants (DE VRIES 1924 c). The conformity is thus seen to be as close as might be expected. The mutants were of the ordinary types, namely, *hamata* on the first bed, one *semigigas* in each of the last three beds and *liquida*, *pulla* and *pallescens* in cultures No. 4 and No. 5.

Oenothera semigigas MUT. *cana*

From the cross with *velutina*, already cited, we had eight specimens of *cana*, all of them with 15 chromosomes and of a pure type. Six plants produced a sufficient supply of seeds, but with only a small germinating power. All of the seeds were sown and all of the seedlings planted out. Counted during the flowering period they gave the results presented in table 2.

TABLE 2

Oenothera semigigas mut. cana. Second generation.

Cana PARENT	TOTAL	*Lamarckiana*	*Cana*	MUTANTS
No. 1	59	28	20	11
No. 2	23	12	9	2
No. 3	28	16	7	5
No. 4	27	13	9	5
No. 5	6	3	3	0
No. 6	5	1	4	0
Total	148	73	52	23
Percentage		49	35	16

For my race of *cana* the corresponding numbers were almost the same, namely, 62 percent *Lamarckiana*, 33 percent *cana* and 5 percent of mutants (DE VRIES 1916 a, pp. 254, 256). Of the mutants in the cultures of 1924 a relatively large number were dwarfs, namely, 8 in the first, and 5 in the fourth, experiment, or 14 and 15 percent. This fact is easily explained by assuming that their parent plants in 1923 were half-mutants for this character and split according to the ordinary rules. The remaining mutants were *pallescens*, *spathulata*, *hamata* in No. 1, *oblonga* in No. 2 and No. 3, and four *auricula* in No. 3. Besides those given in our table, there was a *cana* with 15 chromosomes, which produced 154 seedlings, almost all of which showed the type of the parent plants, only two having the marks of *Oe. Lamarckiana*. Moreover, there was a large amount of barren grains (76 percent). I also sowed the seeds of two specimens of *cana linearis* derived from the cross of *Oe. semigigas*×*blandina*. As was to be anticipated, they produced the type *blandina laeta* instead of *Lamarckiana*, and of this 25 and 17 specimens out of a total of 66 and 60, and besides these 30 and 39 plants of the type of *blandina*. The remainder were 8 and 4 *cana linearis*, 2 *pallescens* and 1 *spathulata*. These figures are therefore to be considered as a corroboration of the main result.

Oenothera semigigas MUT. *liquida*

From the cross with *velutina*, I selfed five plants out of the seven of *liquida* of a pure type and with 15 chromosomes (DE VRIES 1924 b, p. 261). There was some difference in their spikes; that of one plant (No. 1) was as compact as in my old race, while the four remaining specimens (Nos. 2 to 5 of the table) had looser racemes. The same difference was seen among four plants from the cross with *tardescens* (DE VRIES 1924 b, p. 224), of which one (No. 6) had a dense spike and three (Nos. 7 to 9) a loose spike. This variation, however, did not seem to have any influence on the genetic constitution, as will be seen from table 3.

For Nos. 2 to 5 the number of barren seeds has been determined and found to be 61, 75, 86 and 81, or on the average 76 percent. This is rather a high figure, but for my race of *liquida* it was almost exactly the same, namely, 78 percent (DE VRIES 1916 b, p. 261). Besides these, the constitution of my race was, on the average, 67 percent *Lamarckiana*, 32 percent *liquida* and 1 percent mutants (DE VRIES 1916 a, pp. 268-269), agreeing sufficiently with the figures of table 3. In the cultures of 1924 the mutants were for a large part *oblonga*, and besides these, one *pallescens*, one *hamata*, one *nanella*, six *pulla*, one *semigigas* and some belonging to types not yet described.

Oenothera semigigas MUT. *spathulata*

Among the mutants of *Oe. semigigas* × *velutina* four specimens of *spathulata* with 15 chromosomes and of a pure type have been recorded (DE VRIES 1924 b, p. 261). They had, however, no good pollen and were therefore fertilized by means of *Oe. blandina*. This change from the

TABLE 3

Oenothera semigigas mut. liquida. Second generation.

Liquida PARENT	TOTAL	*Lamarckiana*	*Liquida*	MUTANTS
No. 1	29	24	4	1
No. 2	60	47	7	6
No. 3	59	49	8	2
No. 4	60	52	6	2
No. 5	60	47	10	3
No. 6	60	49	7	4
No. 7	61	43	12	6
No. 8	58	39	12	8
No. 9	59	32	16	11
Total	507	382	82	43
Percentage		76	16	8

ordinary method of self-fertilizing must result in two main changes in the progeny. Instead of specimens of the type of *Lamarckiana*, the well known hybrid, *Oe.* (*Lamarckiana* × *blandina*) *laeta*, must arise, and instead of the barren grains of *velutina* × *velutina*, viable seedlings with the characters of *Oe. blandina* must be found. According to the preferential fertilization of this latter (DE VRIES 1924 a) the *blandina* plants will occur in relatively too high numbers. There were still some empty grains, reaching 30 to 52 percent of the harvest, but these were evidently due to the weak condition of the type. The offspring of the four mutants flowered for the larger part in 1924 and yielded the figures of table 4.

TABLE 4

Oenothera semigigas mut. spathulata after fertilization by Oenothera blandina.

Spathulata PARENT	TOTAL	*Laeta*	*Blandina*	*Spathulata*	MUTANTS
No. 1	58	13	40	3	2
No. 2	63	0	47	5	11
No. 3	68	11	41	10	6
No. 4	59	20	21	15	3
Total	248	44	149	33	22
Percentage		18	60	13	9

In my previous race of *Oe. spathulata*×*blandina* I counted 25 percent of barren grains, and among the viable germs I observed 30 percent *laeta*, 52 percent *blandina*, 18 percent *spathulata* and very few mutants (DE VRIES 1924 b, p. 213). The constitution of the mutants from *semigigas* may therefore be considered as sensibly the same as that of the race. The mutants in the cultures of 1924 were 1 *lata*, 3 *auricula*, 2 *hamata*, 1 *liquida*, and in the second and third experiment 10 plants of a uniform but new type, with small, rounded and shiny leaves.

Oenothera semigigas MUT. *hamata*

Under this name I have described a very rare mutant, which, however, originated from different strains (DE VRIES 1924 b, p. 216). The same type is, curiously enough, not at all rare among the mutants from *Oe. semigigas*. From the cross with *velutina* I had two flowering specimens of a pure type and with 15 chromosomes (DE VRIES 1924 b, p. 261), which gave, after self-fertilization, a progeny whose constitution is shown in table 5.

TABLE 5

Oenothera semigigas mut. hamata. Second generation.

Hamata PARENT	TOTAL	*Lamarckiana*	*Hamata*	MUTANTS
No. 1	58	48	9	1
No. 2	3		2	1
Total	61	48	11	2
Percentage		79	18	3

My race of this name had given, as an average from two generations, 82 percent *Lamarckiana* and 31 percent *hamata*, besides about one-half of barren seeds. The constitution of the new mutants was, therefore, sufficiently the same as that of the race. Both were splitting mutants of the ordinary dimorphic type. The mutants were, in 1924, one *liquida* and one of the form of *diluta*.

Oenothera semigigas MUT. *pulla*

This type, which has not been remarked until very recently, is now easily recognized in the phase of the rosettes as well as during the time of flowering (DE VRIES 1924 b, p. 229; DE VRIES and BOEDIJN 1924 b, pp. 261, 266, fig. 2). It reaches half the height of the parent species, is hardly branched and has long, narrow, conical flower-buds with a reddish tinge. It is rich in pollen and in seeds. In the table given by BOEDIJN and myself (1924 b, p. 261) five specimens with 15 chromosomes and of a pure type

have been mentioned. I have self-fertilized them in 1923 and got in the next summer the results shown in table 6.

TABLE 6

Oenothera semigigas mut. pulla. Second generation.

Pulla PARENT	TOTAL	*Lamarckiana*	*Pulla*	MUTANTS
No. 1	88	40	33	15
No. 2	125	106	17	2
No. 3	135	123	10	2
No. 4	158	127	25	6
No. 5	155	132	17	6
Total	661	528	102	31
Percentage		80	15	5

I have made a control experiment with my race of this name, which originated directly from *Oe. Lamarckiana*, and which is to be described elsewhere, and found as an average from the offspring of two parent plants, 34 percent *Lamarckiana*, 40 percent *pulla*, and 26 percent of mutants. The constitution is thus sufficiently proven to be the same in both cases. The amount of barren grains was 50 percent for the race and 38 percent (27 to 48 percent) as an average for the five specimens referred to. The mutants of 1924 were 2 *albida*, 5 *oblonga*, 7 *auricula*, 7 *cana*, 4 *pallescens*, 1 *spathulata* and 5 *nanella*. Evidently they showed the same range as the ordinary mutants from *Oe. Lamarckiana* and no other types occurred. Like the primary forms of the six other main clasess, the *pulla*, which is the only trisomic mutant in the central group, is a dimorphic form, giving one-half of empty seeds and reproducing from the other half, partly its own type, and partly that of the parent species.

MUTANTS OF THE TYPE SESQUIPLEX

In a previous article I have proposed this name for those mutants which have about one-half of empty seeds, but are constant and uniform in their living progeny (DE VRIES 1923 a). Their genetical constitution is usually either (mutant + *laeta*) × *laeta*, or (mutant + *velutina*) × *velutina*. They are dominant, the mutated gametes reproducing the race, whereas *velutina* × *velutina*, and *laeta* × *laeta* give the barren grains.

Among the mutants from *Oe. semigigas* such *sesquiplex* forms rarely occur, or perhaps are not always easily recognized. I selected two of them with 15 chromosomes, namely, *oblonga* and *auricula* (DE VRIES 1924 b, p. 261) for self-fertilization. Moreover, two specimens of *cana* with a deviating type, but with the same number of chromosomes (DE

VRIES 1924 b, p. 261) were found, after self-fertilization, to have a uniform progeny, besides a few mutants, and therefore to belong to this category. For convenience's sake I shall distinguish them by the name of *cana sesquiplex*. They reached about one-half the height of normal *cana* and had thicker fruits, which were almost like those of *Oe. Lamarckiana*. The results are in table 7.

TABLE 7

Sesquiplex mutants of Oenothera semigigas. Second generation.

MUTANTS	TOTAL	*Oblonga*	*Auricula*	*Cana Sesquiplex*	MUTANTS
Oblonga.....	84	83	..	..	1
Auricula.....	57	..	57	..	..
Cana sesquiplex..	59	..	..	56	3
Cana sesquiplex..	58	..	..	54	4
Total.....	258	83	57	110	8
Percentage.....					3

The amount of barren grains was, for *oblonga*, 69 percent, for *auricula*, 52, and for *cana sesquiplex*, 73 and 81 percent. Since the non-mutated gametes must have been of the *velutina* type, which is usually preferred during fertilization (DE VRIES 1924 a), these numbers must be considered as being too high, and as pointing to the expected figure of one-half of barren seeds. Setting aside these and the mutants, the four lines were found to be uniform. The mutants were 1 *albida*, 1 *scintillans* and 3 *oblonga*.

16- AND 17-CHROMOSOME MUTANTS OF *Oenothera semigigas*

All of the mutants of *Oe. semigigas* dealt with in the above tables and descriptions had 15 chromosomes in their nuclei, as far as investigated. Besides them, I succeeded in getting a sufficient harvest from four specimens with 16 or 17 chromosomes, derived from the cross *Oe. semigigas* × (*biennis* × *Lamarckiana*) *velutina* and from two plants of the *cana* type, from the cross *Oe. semigigas* × *tardescens*, which behaved like them in their progeny, but whose chromosomes, unfortunately, have not been counted.

If the doubling of the chromosomes may be considered as an indication of a specific mutation, we should conclude that in the 16- and 17-chromosome mutants, two or three chromosomes, respectively, were in this condition. And if the application of the law of probability to the distribution of the mutations among the egg-cells of *Oe. semigigas*, as proposed by BOEDIJN and myself (1924 b), holds good in these instances, we must

expect that among the progeny of such plants the two or three mutated types, respectively, might separate and be seen each for itself. This is, however, not always the case. The dominant type is repeated in about the expected percentage, but the second form is either absent, or concealed in a few specimens among the other mutants, or shows in too small figures. Only in one instance it was plentiful, as will be seen in table 8. The third type, to be expected from the 17-chromosome mutants, has not shown itself clearly in the experiments here to be recorded. It seems probable that the second and third type suffer in a larger degree from the mortality of the germs within the seeds of *Oe. semigigas*, which is different for different categories, as will be shown elsewhere. But why this should be so, remains an open question.

In table 8 the type of the parent plants is introduced as "main type," while of the other types, aside from *Lamarckiana*, that form is considered to be a "second type," which occurred in the largest number of individuals. The remainder are given under the head of "mutants." In this table the mutants are given for each of the cultures, since they might include a

TABLE 8

16- and 17-chromosome offspring of Oe. semigigas. Second generation.

PARENTS	NUMBER OF CHROMOSOMES	TOTAL	*Lamarckiana*	MAIN TYPE	SECOND TYPE	MUTANTS	TOTAL MUTANTS
Liquida...	16	81	26	4 *liquida*	42 *oblonga*	1 *albida*, 1 *auricula*, 1 *semigigas*, 6 *pulla*	9
Pulla....	16	59	25	29 *pulla*	..	1 *albida*, 1 *auricula*, 1 *pallescens*, 2 *nanella*	5
Pulla...	17	60	39	18 *pulla*	..	1 *auricula*, 1 *semigigas*, 1 *nanella*	3
Auricula..	17	55	..	51 *auricula*	4 *oblonga*	.....	0
Cana.....	..	77	39	21 *cana*	5 *auricula*	1 *albida*, 2 *oblonga*, 8 *nanella*, 1 *rubrinervis*	12
Cana.....	..	57	13	26 *cana*	12 *auricula*	1 *albida*, 3 *pallescens*, 1 *spathulata*, 1 *nanella*	6

third type in one or more of the four last-named cultures. The number of chromosomes was 16 in the first two and 17 in the following two parent plants. The *nanella* and *rubrinervis* are mutants of the central group, having only 14 chromosomes; therefore, they cannot be included in this discussion. The other mutants were *albida*, *auricula*, *pulla*, *pallescens*, *oblonga*, *spathulata* and *semigigas*. The chance of finding a "third type" among the progeny of No. 3 and No. 4 is, however, very small, since

there occurred only one trisomic mutation, namely, *auricula* in one of them, and none in the other. It is to be noted that the second types of our table are secondary forms of the class of *scintillans*, and that for the *pulla*, also, *auricula* has been observed among the mutants, although only in one individual for each. Perhaps the viability for second types is the largest in this group, as it has often been for *scintillans* itself and for its secondary forms in analogous experiments. In experiment No. 5 eight dwarfs have been observed, or about 10 percent, and this points to the condition of the parent plant as that of a half-mutant for this factor, as has been discussed above under the head of, *Oe. semigigas* mut. *cana*.

I have cultivated the offspring of a cross, *Oe. pulla* × *blandina*, in which the female parent had also 16 chromosomes. Among 60 offspring, however, here also no second type was seen. There were 8 *pulla* and no mutants, the remaining 52 individuals having the characters of *Oe.* (*Lamarckiana* × *blandina*) *laeta*, as was to be expected.

Among the offspring of *Oe. semigigas* × *blandina* I self-fertilized two beautiful plants of *hamata* and had a second generation of 58 and 59 individuals, respectively. Among these, 6 and 11 were like the parent, but 10 and 8 were *cana*, which might be considered as a second type and thus give a corroboration of the conclusions given above. There were 23 and 5 *blandina-laeta* and 16 and 25 *blandina*, as might be expected. In the first culture there were three mutants (*lata*, *pallescens* and *nanella*) and in the second, 10 dwarfs, pointing to a condition of a half-mutant for this factor in the parent plant, as discussed under the head of "*cana*."

INTERCHROMOSOMAL CORRELATIONS

Almost all the cultures described above produced a large number of mutants besides the main types. The percentages did not essentially differ from those of *Lamarckiana*, and the same forms were present in almost every single instance, although the size of the experiments was too small for the expectation of complete series. But all of the primaries occurred, namely, *lata*, *scintillans*, *cana*, *liquida*, *pallescens*, *spathulata* and *pulla*, also both the accessories, *albida* and *oblonga*. Nor did *semigigas* fail, and *nanella* occurred either as such or as half-mutants (as in the experiment with *cana*). From this we may conclude that the activation of one of the primaries or accessories in one of the chromosomes does not change the mutability of the others. This condition remains the same as it has been found in the parent species, *Oe. Lamarckiana*.

In this respect the trisomic or specific mutations are essentially different from the homogeneous or homozygotic types, previously described

(DE VRIES 1923 c, p. 221). *Oe. blandina*, *Oe. deserens* and *Oe. decipiens* have produced, until now, almost no mutations, even in cultures of a large size. If crossed with one another, the progeny also shows no mutability, either in the first or in the second generation. Over 350 mostly flowering hybrids have been studied for each of the two, embracing the six possible combinations. Here, therefore, is a clear proof of interference, especially when we compare this absence of mutability with the mutability shown in the tables of the present article. Of the homogeneous mutations mentioned, *Oe. blandina* belongs to the class of *velutina*, but *Oe. decipiens* and *Oe. deserens* to that of *laeta*. All of them lack both the zygotic lethals which are characteristic for the parent species. The factor-complexes of all three must be assumed to be represented in the central pair of chromosomes, which also carries the lethal factors, as BOEDIJN and I (1923, 1924b) have shown. Those complexes are of a recessive nature. From this we see that the operative condition of these recessives in the central chromosome hinders the mutability of the lateral ones in producing its types. In other words, there exists an interchromosomal correlation between the central rod and the lateral ones, which is absent between the lateral rods among themselves.

The latent condition of the mutability of *Oe. Lamarckiana gigas* discovered by means of double crossing (DE VRIES 1924b) may be due to such a form of correlation, and this would point to the possibility of some degree of latent mutability existing in numerous other cases, where plants have been considered until now as immutable.

14-CHROMOSOME OFFSPRING OF *Oenothera semigigas*

These have ordinarily the type of *Oe. Lamarckiana* and should be expected to come true to their type after self-fertilization. This proved to be true in the cultures of the offspring of three such plants and of two others, whose chromosomes had not been counted. Each experiment embraced about 60 flowering individuals. Mutants or aberrant types were not seen in the first-named three lines, but included in the two others, 1 *auricula* and 1 *cana* in the first, and 2 *lata*, 3 *albida*, 2 *scintillans* and 2 *cana* in the second instance. Leaving these aside, all of the 300 plants were uniform and pure *Lamarckiana*.

Among the offspring of *Oe. semigigas*×*tardescens* I had noted one plant which had the external marks of *Oe. rubrinervis* (DE VRIES 1924 b, p. 225). I sowed its seeds after fertilization and had in 1924 a progeny of 59 plants, 54 of which were like the parent and as brittle as my race of that name, while five were mutants (2 *oblonga* and 3 *liquida*).

CONCLUSION

The offspring of *Oe. semigigas*, after fertilization with the pollen of a *velutina* type (*biennis*×*Lamarckiana-velutina*, *tardescens* or *blandina*), shows the same hereditary constitution as the corresponding older races. The dimorphic mutants split into *Lamarckiana* and their own type (*scintillans*, *cana*, *liquida*, *spathulata* and *pulla*), the *sesquiplex* forms give a uniform progeny besides about one-half of empty seeds (*oblonga*, *auricula*, and the new form *cana sesquiplex*). Derivatives with 14 chromosomes also give a uniform offspring, with some mutants. Those with 16 or 17 chromosomes might be expected to split into two or three forms each, but they repeat their main type and give a second one only rarely and then mostly in very small numbers of individuals.

All in all, the mutants derived from *Oe. Lamarckiana semigigas* are genetically constituted, as far as investigated, exactly like the corresponding mutant races, directly sprung from the parent species. Interchromosomal correlations have not been found between them.

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THE FACTORS OF THE ALBINO SERIES OF GUINEA-PIGS AND THEIR EFFECTS ON BLACK AND YELLOW PIGMENTATION

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INTRODUCTION

Genetic studies on various animals have shown that albinism is the extreme in a series of grades of dilution of color and that it is independent, genetically, of white spotting, the "partial" albinism of many authors. Albinism and its allelomorphs affect the intensity of all kinds of melanin pigmentation,—black, yellow, brown, etc., and affect all parts of the body in which such pigment occurs, but most conspicuously the skin, fur and eyes. They have no effect on the localization of the different kinds of pigment. The highest allelomorph in guinea-pigs, for example, is found alike in golden agoutis, blacks, reds and black-red tortoise-shells, which are all "intense" varieties, while a lower allelomorph is found, alike, in yellow agoutis, sepias, yellows, and sepia-yellow tortoise-shells, which are all "dilute" varieties.

The general nature of the effects suggests that the albino series has to do simply with the rate of some process which is essential to all melanin pigmentation. On this hypothesis, one might expect to be able to arrange the compounds in a certain order of intensity of color. This, however,

turns out not to be possible. In a description of four allelomorphs in this series in guinea-pigs (WRIGHT 1916) it was shown that a compound with a more intense yellow than another might have a less intense black. The intensities of black, of yellow and of eye color in the various compounds were described as in table 1.

TABLE 1

COMPOUND	YELLOW FUR	BLACK FUR	EYE COLOR
C—	Red	Black	Black
$c^d c^d$	Yellow	Dark sepia	Black
$c^d c^r$	Cream	Dark sepia	Black
$c^d c^a$	Cream	Light sepia	Black
$c^r c^r$	White	Dark sepia	Red
$c^r c^a$	White	Light sepia	Red
$c^a c^a$	White	White	Pink

The homozygous red-eyed dilutes, $c^r c^r$, were found to lack the power to produce yellow, the parts of the fur which would otherwise be yellow being white, yet they were much blacker in the black parts of the fur than the black-eyed dilutes carrying albinism ($c^d c^a$) which nevertheless had the power to produce a pale yellow or "cream."

It was recognized that this result could be interpreted as meaning that the factors of the albino series act independently on eye color, black in the fur, and yellow in the fur, or indeed, that the so-called allelomorphs are merely combinations of very closely linked factors with no necessary similarity in physiological effect. The writer preferred the view, however, that the factors of the albino series have a single effect on pigmentation and that the irregularities in the order of effect in different cases are due to secondary processes in the physiology of pigment production. It was suggested first that the threshold for yellow is higher than that for black; second, that above the threshold for yellow its process of production interferes with the production of black even in black parts of the coat; and finally, that conditions relative to the threshold of yellow are different in eye and skin.

Since this paper was written, a fifth allelomorph of the albino series has been found in guinea-pigs (WRIGHT 1923). A fourth (chinchilla) has been added in rabbits to the long-known series, intense, Himalayan and albino (CASTLE 1921), and multiple allelomorphs of albinism have been found in rats (WHITING and KING 1918) and in mice (DETLEFSEN 1921, FELDMAN 1922).

The purpose of the present paper is to present more fully than before the evidence on the allelomorphism of the five factors in the guinea-pig together with a study of the average intensity of black and yellow in each of the fifteen compounds now known.

MATERIAL

Three albino-series allelomorphs have been found in the stock of guinea-pigs maintained by the Bureau of Animal Industry. These are the "intensity" factor, C, the new "dark-dilution" factor, c^k, and albinism, c^a. A few animals with "light dilution," c^d, and "red-eyed dilution," c^r, were kindly presented by Professor CASTLE and are the sole sources of these factors in the present experiments. The light dilutes traced to Professor CASTLE'S "dilute selection" stock which was the principal source of the animals used by the writer in the experiments described in the paper of 1916. It should be added that one of the animals sent by Professor CASTLE, an animal descended from his importations from Arequipa, Peru (CASTLE 1916), transmitted a dark dilution apparently identical with c^k from the stock of the Bureau of Animal Industry. The dark dilutes described in the present paper, however, all owe their dilution factor to the Bureau stock rather than to this source. The present discussion will be based primarily on the data from 192 matings in certain experiments (J and K) the chief purpose of which was the study of the effects of the albino series on black and yellow. All young born in these experiments, from their beginning in 1919 to the end of 1923, are included in the data as far as their records are complete, with two classes of exceptions.

One of these includes all descendants of a certain male whose appearance and breeding record constitute the only clear exception to the ordinary mode of inheritance of the five allelomorphs, which the writer has observed. This male was produced by dilute parents ($c^dc^d \times c^dc^r$) in another experiment. He attracted attention when first recorded, as an intense-dilute mosaic, somatically, an extremely rare condition. In matings with lower recessives (albinos, c^ac^a, and red-eyed dilutes, c^rc^a) he produced both intense and dark-eyed-dilute young. The occurrence of the intense young (C—) proves him to have been a mutant, while the ratio, 79 intense to 149 dilute, departs so widely from equality as to indicate that he was a germinal as well as a somatic mosaic. There has been great variation in the ratio at different times in the five years during which he has been producing young. Altogether, his case is a very peculiar one and will be described in more detail elsewhere. Both his intense and dilute young and

their descendants have behaved normally. They happened to be recorded in experiment K, but it has seemed best to exclude them from the data to be presented here.

The second class of exceptions includes all animals which descend along any line from a certain mating (B211) which has been the sole source of an independent dilution factor (*f*) (WRIGHT 1923). Nearly all possible combinations between this factor and the albino series have now been made, yielding a number of new color varieties, among which black-eyed silver agoutis ($c^kc^aff A$—), slightly creamy black-eyed whites (c^dc^dffee), pink-eyed cream-yellow mosaics (C—$ffpp$) and a new kind of apparent albino (c^dc^affpp) may be mentioned. While all of the data are in harmony with those presented here, it has seemed best to avoid discussion of the complications arising from the bringing together of two dilution series whose effects simulate each other more or less.

There is a great deal of data on the albino series from experiments carried on for other purposes. As far as this has been critically analyzed, it is all in harmony with the data from experiments J and K except for the mutant male referred to above. It will be convenient to use certain of these data to supplement the rather scanty data from experiments J and K as regards the intensity of sepia in certain compounds, especially c^kc^r and c^kc^k. The purpose of experiment L has been to make all combinations between the albino series and the "pink-eye" factor (*p*). In experiment N, all combinations between the albino series and the brown factor (*b*) have been made. Experiment UR includes matings leading up to the production of a stock recessive in eight sets of factors. The matings of these experiments have been analyzed critically for the source of the albino-series factors involved and with respect to the appearance and breeding record of all descendants. Use is made here only of animals of known constitution, which showed sepia in the fur (factors *p* and *b* absent).

Experiments J and K were largely a self-contained group of matings. The matings made in 1923 had on the average between 4 and 5 generations of ancestry of J or K matings. As homozygous stocks were not available for starting the experiments, most of the early matings produced more than one class of progeny. It was thus necessary to mate many animals whose genetic constitution was not uniquely determined from their parentage. A genetic constitution has been assigned each mated animal only after an exhaustive investigation. That assigned is in every case consistent with the constitutions assigned the parents and all of their ancestors as far back as known, with its own color within the range of

variation of the various compounds, with the classes of progeny produced and with all later descendants. As to color, there is, as will be seen, considerable overlapping of the various compounds, especially with respect to sepia. The following statements may be made here: Intense red in any part of the coat occurs only in the presence of the intensity factor *C*; yellow or cream (in the present experiments) only with c^k or c^d as the highest member of the series present; a white brindle (tortoise-shell pattern) associated with more or less dark-red eyes only with c^r as the highest member.

Pink-eyed white in the present data has always meant a true albino ($c^a c^a$), although in other experiments such combinations as *c*^{r}*c*^{r}*ppee* (IBSEN 1919) and $c^d c^a ffpp$ have been responsible for apparent albinos.

The factors most difficult to distinguish by appearance have been the two dilution factors c^k and c^d. In the great majority of cases, however, the matings have been made in such a way that a black-eyed dilute could be definitely assigned to one or the other by its ancestry alone.

The evidence for the allelomorphism of the five factors will be considered chiefly from the standpoint of particular critical crosses. It may be noted here, however, that the consistency of the results within a large net-work of matings such as represented by experiments J and K affords perhaps the most convincing evidence, but evidence of a kind which it is difficult to present in a compact form. The great variety of crosses which have been made and the consistency of the results with the hypothesis of allelomorphism may be seen, however, from tables 13 to 20 which give all of the data in experiments J and K through 1923 with the exceptions previously noted.

METHOD OF GRADING

Series of sepia and yellow skins have been used for grading the intensity of the colors. The sepia series runs from 3 for a light sepia to 14 for intense black. The yellow series runs from grade 3 for a light cream to 13 for the most intense red. Each series gives the appearance of a nearly continuous gradation.

A guinea-pig which has a reasonably large amount of sepia or yellow in a compact spot can easily be graded, with only an occasional question of one grade. Sepia can not, however, be graded satisfactorily in agoutis because of the replacement of the blackest part of each hair by yellow. Consequently, no attempt has been made to assign them sepia grades. Non-agouti tortoise-shells (*aa e'e'*) have been given preference in the matings in order to obtain animals which could be graded with respect to

both sepia and yellow as far as possible. Many agoutis, self-yellows and self-sepias came in the early generations, however, because of the association of c^d and c^r with the factors determining these patterns in the foundation animals.

There has been considerable difficulty in keeping a constant set of sepia grades. It has been found that the sepia skins gradually fade and become browner, making necessary restandardization from time to time. Errors in grading from this cause probably make each class appear slightly more variable than it really is. Comparison of class averages for different years shows, however, that there has been no serious error in averages due to this cause. There has been no such tendency to fade among the yellow standards. Grades 7, 10 and 13 were taken from three inbred families, No. 35 (c^kc^k), No. 2 (CC) and No. 32 (also CC). The guinea-pigs of these families are uniform in intensity of color at any given time and can safely be assumed to be so from year to year. Frequent comparison of the standards with living young from these families make it certain that there has been no change in the meaning of the yellow grades.

The grades based on comparison with standard skins have all been made by the writer. There are additional data, useful in connection with the young which died before the accurate grade was given, in the color terms in the daily record of births kept by Mr. O. N. EATON. These color terms are given simply by inspection. While there is naturally some overlapping, it is found that in general they compare with the numerical grades as follows:

Color	*Grade*	*Color*	*Grade*
Light sepia	3–6	Cream	3–5
Medium sepia	7–10	Yellow	6–8
Dark sepia	11–12	Red	9–13
Black	13–14		

CHANGE IN COLOR WITH AGE AND EFFECT OF COLD

Unless otherwise stated, all grades refer to the color within a week or two after birth. There is seldom any change in the grade of yellow later in life but the sepias regularly become darker. This effect is greatest in the red-eyed varieties. Even the heterozygotes (c^rc^a) usually become a glossy iridescent black, at least on the back, at maturity, while the black-eyed sepias merely become a darker brown. Thus, while a red-eyed sepia c^rc^a usually differs but little from a black-eyed sepia of type c^dc^a at birth, and is distinctly lighter than c^kc^a, at maturity it will in general be found to be the darkest of the three. This darkening of the sepia is probably an effect of cold. In harmony with the experiments of LENZ (1923) and of

SCHULTZ (1918, 1922) on Himalayan rabbits, it has been found that after plucking a patch of hair from a sepia part of the fur, in any of the compounds (including intense blacks, *C*) the new hair, especially in winter, is of a distinctly darker color. It is possible to bring out pale sepia patches in this way even in albinos. In agreement with the natural age effect the darkening is greatest in red-eyed dilutes.

If yellow hair is plucked, either there is no visible difference between the new hair and that around it, or the former comes out slightly lighter in color.

The grades in the series of skins used here were defined without relation to the grades used in the previous study (WRIGHT 1916). They compare approximately as follows (the comparison with RIDGWAY'S color charts as given in the above paper is repeated):

Grades of sepia

1916	1925	RIDGWAY
Black 0	14	Black
Sepia 3	10	16‴n, warmer and darker than clove brown 17‴m.
Sepia 6	6	16‴l, warmer and lighter than clove brown 17‴m.
Sepia 9	3	17‴i, hair brown, somewhat purer, however.

Grades of yellow

1916	1925	RIDGWAY
Red 0	11	15′i, ochraceous tawny.
Yellow 3	7	16″b, redder than cinnamon buff 17″b.
Cream 6	4	19″b, cartridge buff.

COMPOUNDS c^kc^a AND c^dc^a

The distinction between the two dilution factors, c^k of the Bureau stock and c^d of Professor CASTLE'S stock, was demonstrated by crossing dilutes from each source with albinos whose sire or dam was a dilute of the other kind (WRIGHT 1923). The process was repeated generation after generation. If the difference in intensity were due to independent modifying factors, the latter should be transmissible through the albinos as well as through the dilutes themselves and the two sets of matings should give identical results. If, on the other hand, the two types of dilution are due to different allelomorphs of albinism, albinos should not be able to transmit their difference, and the results of the two sets of matings should maintain their distinctness. The latter turned out to be the case (Table 2).

All but one of the 77 graded sepias from matings of type 1 were below grade 10 in intensity. Among those which were not graded, 7 were called light or medium sepias at birth by Mr. EATON and only one, found dead at birth and probably wet, was called a black-cream. Two had no sepia in the fur. The sepias from matings of type 2, on the other hand, were graded

between 10 and 13. Of those not graded, 12 were called dark sepia or black by Mr. EATON, 6 had no sepia in the fur and only one was called medium sepia. Thus, with a few doubtful exceptions, light and medium sepias have produced only light and medium sepias (and albinos), and dark sepias have produced only dark sepias (and albinos) in matings with albinos, regardless of the ancestry of the albino parent. These results demonstrate that c^d and c^k are different allelomorphs of albinism.[1]

TABLE 2

The grades of sepia among the young from matings between dilutes, heterozygous for albinism, and albinos. In matings of type 1, the dilutes (light sepia and cream) trace their dilution to Prof. CASTLE'S *dilute selection stock while in the matings of type 2 the dilutes (dark sepia and cream) trace their dilution to Bureau stock. Each type of dilute is mated with albinos produced by the other type of mating. The young not graded either had no sepia in the coat or died too soon.*

TYPE NUMBER	MATING	GRADE OF SEPIA												NOT GRADED	DILUTES		TOTAL DILUTES	ALBINO
		3	4	5	6	7	8	9	10	11	12	13	14		3–9	10–13		
1	c^dc^a (from 1) $\times c^ac^a$ (from 2)	1	3	6	8	22	34	2	1	..	..	..	..	10	76	1	87	105
2	c^kc^a (from 2) $\times c^ac^a$ (from 1)	..	..	..	..	..	..	..	7	15	34	10	..	19	..	66	85	77

TABLE 3

The same matings as in table 2, but with the young classified with respect to grade of yellow instead of black.

TYPE NUMBER	MATING	GRADES OF YELLOW											NOT GRADED	TOTAL DILUTES	ALBINO
		3	4	5	6	7	8	9	10	11	12	13			
1	c^dc^a (from 1) $\times c^ac^a$ (from 2)	2	53	6	..	..	..	..	..	..	..	..	26	87	105
2	c^kc^a (from 2) $\times c^ac^a$ (from 1)	..	24	23	5	..	..	..	..	..	..	..	33	85	77

The grades of the creams from these matings are shown in table 3. There appears to be a slight difference in average grade, but there is so much overlapping that the grade of cream is practically worthless as a means of distinguishing c^dc^a and c^kc^a.

Types c^dc^a and c^kc^a have been obtained from other matings. The grades of those which came from matings which could produce no other dark-eyed

[1] The reciprocal matings, female albino by male dilute and female dilute by male albino, are combined. This is justified by the absence of sex-linked inheritance in this case and the absence of appreciable sex differences in intensity of color. Matings of type $c^dc^a \times c^ac^a$ produced 24 dilute sons, 25 dilute daughters, 28 albino sons and 26 albino daughters. The reciprocal matings produced 13 dilute sons, 25 dilute daughters, 22 albino sons and 29 albino daughters. The average grades of the sons were sepia 7.31, cream 4.00, those of the daughters were sepia 6.95, cream 4.11. No distinction of sex has seemed necessary in the later tables.

type of dilute are given in groups A (experiments J and K) and C (experiments L, N and UR) in tables 9 and 10 (see appendix). The numbers are considerably larger than the special crosses given in tables 2 and 3, but the results are essentially the same. There is still only one example of overlapping in grade of sepia, a c^dc^a of grade 10. The assignments to types c^dc^a and c^kc^a from matings which produced more than one type of black-eyed dilute, as given in groups B and D in tables 9 and 10, are consistent with the figures for those of more certain constitution. The grand totals are given in tables 11 and 12.

TABLE 4

The grades of yellow among the progeny of matings between black-eyed dilutes heterozygous for albinism (c^kc^a or c^dc^a).

MATING	GRADE OF YELLOW											NOT GRADED			c^kc^k	c^kc^a	c^ac^a
	3	4	5	6	7	8	9	10	11	12	13	Cream	Yellow	No yellow			
$c^dc^a \times c^dc^a$	2	42	11	4	17	2	..	..	..	..	..	15	7	15	37	78	24
$c^kc^a \times c^kc^a$	..	13	12	3	11	2	..	..	..	..	..	1	3	5	17	33	19
$c^kc^a \times c^dc^a$	..	19	9	5	11	1	..	..	..	..	..	1	4	1	18	33*	10

* Composed of 20 c^kc^a and 13 c^dc^a as indicated by grade of sepia.

COMPOUNDS c^kc^k, c^kc^d AND c^dc^d

On crossing dilutes from matings of type 1 with each other ($c^dc^a \times c^dc^a$) it is found that a considerable number of the young are well outside the limits of variation of c^dc^a, being more intense in both the sepia and yellow parts of the fur than their parents. Closely similar results have been obtained from matings of types $c^kc^a \times c^kc^a$ and $c^kc^a \times c^dc^a$. The distribution of the grades of cream and yellow are shown in table 4. Comparison with table 3 suggests that all or nearly all of grades 7 and 8 and probably some of grade 6 (at least in the case of light dilutes) are homozygotes, c^dc^d or c^kc^k, or are heterozygotes between the two types of dilution, c^kc^d. The ratios agree reasonably well with this interpretation. In each of these matings, we have an analogue of the Blue Andalusian fowl case,—cream being the unfixable heterozygote between yellow and white. There was no difficulty in obtaining a reasonably true-breeding strain of medium sepia-yellow color (c^dc^d) by selecting the yellow segregates from the matings between heterozygotes. The distribution of all of definitely known constitution (A, C) or of probable constitution (B, D) are given in tables 9 and 10 (appendix) with grand totals in tables 11 and 12 as before. These show considerable overlapping with c^dc^a with respect to sepia, but only a small amount with respect to yellow. Similar results are shown for c^kc^k and c^kc^d in these tables. A homozygous race of dark dilutes (c^kc^k) has been

developed from segregates in these experiments since the period covered by the data. They are uniformly dull black (usually grade 13) with yellow markings (usually of grade 7 or 8). They agree in these colors with the inbred family (No. 18, now extinct) to which in the main they traced their dilution factor.

Eight of those which, on account of their color, were thought to be c^kc^d, were tested by mating with albinos. As shown in table 13 (appendix), they produced 32 dark dilutes (c^kc^a) and 40 light dilutes (c^dc^a) whose colors, included in group B in tables 9 and 10, were typical of these varieties. The segregation was clear-cut in the litters which contained both kinds.

It may be interesting at this point to summarize in table 5 the intensity relations of the three allelomorphs, c^k, c^d and c^a, indicated by the data so far considered.

TABLE 5

	GRADES OF INTENSITY					
	c^kc^k	c^kc^d	c^dc^d	c^kc^a	c^dc^a	c^ac^a
Sepia.....	13.1	12.4	9.9	11.5	7.0	0.0
Yellow.....	7.1	7.2	7.0	4.6	4.2	0.0

It may be seen that c^k and c^d are almost indistinguishable in effect on yellow. Lumping them together under the symbol c^{kd}, the homozygotes have a yellow of about grade 7.1 and the heterozygotes a cream of about grade 4.4. On the other hand, c^k and c^d differ markedly in effect on black, whether homozygotes or heterozygotes are compared. In relation to each other, c^k seems almost fully dominant over c^d. It must be remembered, however, that the grades are not measurements of the actual amounts of pigment, but are based on a scale in which successive grades can just be distinguished. It is certain that the addition of a given amount of pigment to white or to the lower grades would produce a more easily recognized difference than the addition of the same quantity of pigment higher in the scale. The approach to dominance of c^k may therefore be merely apparent.

There is one other point to which attention may be called. The type c^kc^a is more intense in the sepia parts of the fur than c^dc^d, but less intense in the yellow parts, furnishing another case in which it is impossible to arrange the compounds in a single order of intensity.

COMPOUNDS c^rc^r AND c^rc^a

A series of color varieties with red eyes, in which the yellow parts of the fur are replaced by white, although the black parts remain more or less

intense, seem to trace back exclusively, as far as known in this country, to a few animals which Professor CASTLE obtained in Peru in 1912 (CASTLE 1914). The eyes show more or less black pigment in the iris, but give a red glow from the pupil because of deficient retinal pigmentation. They are thus intermediate between the ordinary dark eyes and the pigmentless eyes of albinos. Evidence that these varieties contain a factor (c^r) allelomorphic with albinism (c^a), dilution (c^d) and full intensity (C) has been presented in previous papers (WRIGHT 1915, 1916, CASTLE 1916). Inspection of tables 8 to 15 will show that the present data are in full agreement with this result. Red-eyed dilutes mated with each other never produce the dark-eyed varieties showing red, yellow or cream in the fur. They segregate as expected in crosses involving the compounds Cc^r, c^kc^r and c^dc^r. It will not be necessary to go into more detail on this point.

Examination of tables 8 to 15 shows a large number of matings which should produce heterozygotes, c^rc^a, but not homozygotes c^rc^r. In other cases, only c^rc^r should appear, while in still other cases both are expected. The red-eyed young which actually appeared where only c^rc^a was expected, were relatively light sepia in color (at birth) with light-red eyes, while those which appeared where only c^rc^r was expected were almost black at birth with dark-red eyes, sometimes difficult to distinguish from the eyes of intense or black-eyed dilute varieties. The actual grades are shown in table 9 (A and C). The table brings out clearly the intermediate character of the heterozygote in grade of sepia, although a small amount of overlapping is indicated.

Matings such as $c^rc^a \times c^rc^a$ produced both types. There is seldom if ever any difficulty in distinguishing the homozygotes from heterozygotes within a given litter. After making as careful a classification as possible on the basis both of grades of sepia and of notes on eye color, mating $c^rc^a \times c^rc^a$ is credited with producing 26 c^rc^r: 50 c^rc^a: 20 c^ac^a in reasonable agreement with expectation. The grand average for intensity of black (table 11) comes out 13.1 for c^rc^r and 8.5 for c^rc^a. There is no trace of yellow in either case in the white regions which correspond to the yellow of other varieties.

COMPOUNDS c^kc^r AND c^dc^r

A considerable number of crosses in experiments J and K were such as to produce only c^dc^r among the dark-eyed dilute varieties. These are brought together in tables 9 and 10 (c^dc^r, row A). Most of them are sepia grade 12 and cream grade 4, the averages being 12.2 and 4.1, respectively. The same result is found among those brought together from experiments UR, L and N (row C in the above tables), the averages again being sepia 12.2

and cream 4.1, respectively. Those assigned to c^dc^r on less certain grounds, in experiments J and K (row B) and UR, L and N (row D), are consistent with the above figures. It will be noticed that c^dc^r has a cream indistinguishable from c^dc^a, but that it has a much darker sepia. In fact, it averages distinctly darker than c^dc^d with respect to sepia, although much lighter with respect to yellow. Curiously enough it is practically indistinguishable from c^kc^a in both sepia and cream, although having no factor in common. A breeding test with albinos, of course, immediately separates them (compare table 13).

No mating in experiments J and K produced c^kc^r as the only expected dark-eyed dilute class. A number were produced by experiments UR, L and N, however, (tables 9 and 10, c^kc^r, row C). They proved to be almost intense black (sepia 13.3) with cream spots (cream 4.5). The results from matings which should produce both c^kc^r and some other dark-eyed class (rows B and D in tables 9 and 10), agree with this result after apportioning the young to the classes as fairly as possible from the expected ratio and the known range of variation of the other dilute class (largely c^kc^a or c^dc^r). A considerable number of those assigned to c^kc^r in experiments J and K on the basis of their appearance, have been mated and have produced young of the expected classes. Thus, 5 thought to be c^kc^r, mated with albinos, produced 23 dark dilutes in the range of variation of c^kc^a and 21 red-eyed light or medium sepias of class c^rc^a.

THE INTENSE COMPOUNDS

It has been pointed out that there is imperfect dominance among the compounds of the four lower allelomorphs in the series, as far as there are recognizable differences in effect. The highest factor, *C*, on the contrary, appears to be completely dominant. Black is represented by intense black, grade 14, in the homozygotes and all of the heterozygotes. There is considerable variation in the grade of red, but no average differences which can be relied upon. Table 10, it is true, shows a slightly higher average for Cc^k than Cc^d or Cc^a, but it happens that the former had a relatively higher percentage of blood from a particular inbred family, No. 32, characterized by a very intense red (grade 13). It has been shown that the difference between this family and certain others (No. 2 and No. 13) characterized by a dull red (grade 10) is inherited independently of albinism. One of these inbred families, No. 13, still occasionally transmits albinism. Inspection gives no indication of a difference between the ordinary homozygotes, *CC*, of this family and those known to transmit albinism, and thus, Cc^a; both are grade 10.

DIFFERENCES WITHIN LITTERS

As previously noted, the comparison of different compounds has been complicated by the presence of modifying factors and by the difficulty in maintaining standard sets of skins, especially in the case of sepia. It seemed of interest, therefore, to make comparisons between the compounds as they segregated out within litters. There is no difficulty in determining which of two young guinea-pigs, compared directly with each other, is the darker, and to measure the difference on the basis of the standard skins. There is, of course, danger of arguing in a circle where the relative intensity of color is both the character which is being studied and the criterion determining genetic constitution. Fortunately, the relative intensity of yellow, regarding which there is seldom any doubt, can be used as the genetic criterion in comparing grades of sepia in many cases. Using compound symbols, there is seldom difficulty in distinguishing the four groups of compounds, $C-$ (red), $c^{kd}c^{kd}$ (yellow) $c^{kd}c^{ra}$ (cream) and $c^{ra}c^{ra}$ (white). In dealing with a mating such as $c^dc^r \times c^dc^r$, it is usually safe to assume that the more intense yellows in a litter are c^dc^d, the less intense, creams, c^dc^r, and those with white in a pattern resembling tortoise-shells and with red eyes, c^rc^r. Comparisons of grades of sepia in the three compounds can be made accordingly.

In cases of segregation in which the grade of yellow is of no assistance, the separation can be made with more or less certainty, depending on the amount of overlapping as found in those of certain constitution. As already noted, there is seldom if ever any uncertainty in separating c^rc^r from c^rc^a, or c^dc^a from any of the compounds c^kc^a, c^dc^r or c^kc^r. It is impossible to separate c^dc^r and c^kc^a with any reliability except by a breeding test and no attempt has been made to do so. In the case of c^kc^r and c^kc^a separation has been attempted, but doubtless with a considerable number of errors, due to overlapping.

Table 21 shows the differences which were found within litters. It is shown, for example, that c^kc^a varied from 3 to 7 grades darker than c^dc^a. In most cases the average difference is very close to the difference between the average grades as given in table 11.

On comparing c^rc^a and c^dc^a as they segregate from the litter, it is found that c^rc^a is not so much darker as the data in table 11 indicate, the difference being only 0.5 instead of 1.5. Indeed, in two cases out of 19, the red-eyed sepia was judged lighter than its dark-eyed litter mate, in nine cases there was no difference and in eight cases the red-eyed sepia was judged darker. On comparing c^dc^d and c^dc^a, on the other hand, a somewhat greater difference was found between litter mates (3.9 grades) than

indicated by the grand average (2.9 grades). These are the most important discrepancies. On the whole, this comparison confirms the grand averages very satisfactorily.

DISCUSSION

The data indicate that there are at least five allelomorphs in the albino series of guinea-pigs. The results could also, of course, be explained by complete linkage among a number of factors, as far as the purely genetic evidence is concerned, but the relations among the characters makes this explanation as artificial here as in the many other cases which have convinced geneticists that multiple allelomorphism is a phenomenon entirely distinct from very close linkage. It is merely necessary to point out that the four recessives resemble each other in general effect, in contrast with the usual lack of correlation between linkage relation and nature of effect, and that none of the recessives are complementary to each other, a surprising coincidence on the linkage hypothesis.

The situation is thus the simplest possible, as far as the mode of inheritance is concerned, but the irregularities in the order of effect of the compounds indicate that it is not so simple with regard to the effects of the factors in development.

The average grades of black and yellow in the fur, and of black in the eyes, are summarized in table 6.

TABLE 6

	BLACK	YELLOW	EYE COLOR
$C-$	14.0	10.6	Black
$c^k c^k$	13.1	7.1	Black
$c^k c^d$	12.4	7.2	Black
$c^k c^r$	13.5	4.6	Black
$c^k c^a$	11.5	4.6	Black
$c^d c^d$	9.9	7.0	Black
$c^d c^r$	12.1	4.1	Black
$c^d c^a$	7.0	4.2	Black
$c^r c^r$	13.1	0	Dark red
$c^r c^a$	8.5	0	Light red
$c^a c^a$	0	0	Pink (no pigment)

Figure 1 presents the relation between intensity of black and yellow, graphically. The impossibility of arranging the compounds in a linear order of intensity is obvious. It may be of interest to point out the

differences in interpretation which would probably have been reached if different pairs of factors had been studied separately. Stocks containing only c^r and c^a or only c^k and c^d would appear to vary only in a modifier of black. Stocks containing only c^k and c^r would seem to involve only a modifier of yellow. With only C and c^d present, the latter would be considered to be a diluter of both black and yellow, while with only c^d and c^r present, c^r would be considered a diluter (or rather annihilator) of yellow, but an intensifier of black.

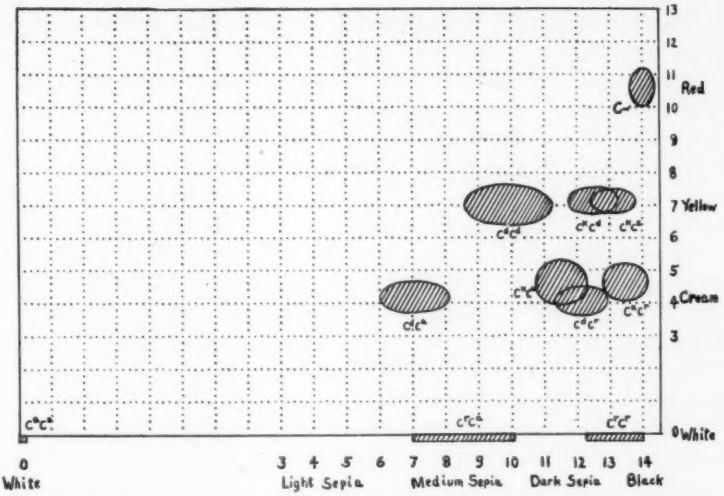

FIGURE 1.—The grades of intensity with respect to both sepia and yellow, of the albino-series compounds of guinea-pigs. The shaded areas extend horizontally to a distance above and below the mean equal to the standard deviation with respect to grade of sepia, and extend vertically the corresponding amount with respect to grade of yellow. This range includes about 68 percent of the individuals. The area should thus include about 47 percent of them.

An explanation of these irregularities may be sought either in the nature of the gene or in its effects on development. The simplest conception of an allelomorphic series is, perhaps, that the different genes differ merely quantitatively. ANDERSON and DEMEREC, in a paper read before the 1921 meeting of the Genetics Sections, and EYSTER (1924) have suggested such an explanation for the constantly mutating allelomorphs involved in the variegation of pericarp color in maize, and STURTEVANT and MORGAN (1923) have shown in the case of bar and ultra-bar in Drosophila, that the latter probably consists merely of two ordinary

bar genes. It would be far from safe, however, to generalize from these peculiarly-behaving cases to multiple allelomorphs in general.

If genes are complex chemical entities, it would seem likely that they would be subject to variation in many different directions. Thus, *a priori*, both quantitative and polymorphic variations seem probable.

Data such as the present can throw no light on these alternatives, since in either case the visible effects may or may not fall into an apparently quantitative series. Thus, however diverse the variations of a gene, if it acts on only one process in ontogeny, the allelomorphs can produce only quantitative differences in that process, and thus are likely to produce a regular gradation in visible effects. If factor *C*, for example, is interpreted as acting on only one fundamental process in the production of melanin pigment, it is quite possible that there may be many diverse modifications of it, each merely weakening this process as far as visible effect is concerned. There may be dozens of distinct albino factors, alike only in that some change in the factor *C* in each case prevents its normal activity. Such allelomorphs could not be separated by breeding tests.

On the other hand, it is quite possible that a purely quantitative series of changes of a gene may be accompanied by polymorphic visible effects, in case the gene affects a number of different but interacting processes in ontogeny with thresholds at different levels of the gene. Thus the nature of the effects in an allelomorphic series gives no evidence on the nature of the gene, but only on the nature of its effects in ontogeny. The question as to the ultimate nature of the differences between factors *C*, c^k, c^d, c^r and c^a may thus be dismissed at this point as one to which the data are not pertinent.

The black and yellow pigments of guinea-pigs are both melanins, and the processes by which they are produced doubtless have much in common. The albino series is not, indeed, the only series which affects them more or less similarly, since the white piebald pattern and white silvering may appear on either a black or yellow ground.

The existence of two series of factors in guinea-pigs (the agouti series A, a', a, and the tortoise-shell series E, e', e), which determine the localization of black and yellow in the fur relative to each other, also indicate a common element. On the other hand, there is considerable independence. Two sets of factors are known in guinea-pigs (the "pink-eye" and "brown" factors), which modify black wherever it occurs (skin, fur and eyes) without any apparent effect on yellow, while one factor (f) is known

which seems to have the opposite effect, to dilute yellow with little if any effect on black.[2]

It would thus be possible to interpret albinism either as affecting a single process fundamental to any melanin pigment production or as affecting the production of black and yellow for different reasons. If the latter be assumed, with the further assumption of polymorphic variation of the gene, the problem raised by the lack of agreement in the order of intensity in black and yellow parts of the fur ceases to exist. Under such conditions there need not be any correlation at all. This dismissal of the whole situation seems rather arbitrary, however, especially in connection with the imperfect correlation between the effects on black pigmentation in the eye and in the fur, and in view of the parallelism between the albino series in different mammals. Without further discussion at this point, it will be assumed, provisionally, that the albino series has only one primary type of effect on pigmentation and that the irregularities in the effects on different kinds of pigment or different parts of the body are due to developmental processes subsequent to the effect of the albino factors.

The first conclusion which is suggested by the data is, that the threshold for yellow is higher than that for black. The red-eyed dilutes (c^rc^r and c^rc^a) may have a great deal of black in the fur, but no yellow. The typically yellow parts of the tortoise-shell or the agouti patterns are represented by pure white. Even albinos develop black in the ears, nose and feet, and sometimes sootiness of the back, but never a trace of yellow. Since this difference in threshold was suggested (WRIGHT 1915) to account for the situation in guinea-pigs and in the Himalayan rabbit, it has been confirmed by the discovery of several albino allelomorphs in other animals in which more or less black is developed, but no yellow. WHITING and KING (1918) found a "ruby-eyed" dilute variety (c^r) of this sort in the wild rat. The homozygotes had light sepia in place of black, but no yellow. The heterozygotes, obtained from matings with albinos, were still paler in color and with brighter-red eyes, in agreement with the imperfect dominance of c^r in guinea-pigs. DETLEFSEN (1921) reported on an allelomorph of albinism (c^d) found in wild mice, apparently intermediate in character

[2] This factor was described in a previous paper (WRIGHT 1923) as diluting yellow and probably intensifying black. The latter conclusion seems now to have been based on an error. A black-cream variety appeared in the progeny of the cross $Cc^aFf \times Cc^dFf$. These were at first thought to be the desired combination c^dc^aff. Breeding tests proved them to be $C-ff$, considerably more extreme in the dilution of yellow than previously observed in this constitution. The combination c^dc^aff has since been produced in considerable numbers and thoroughly tested. It is light sepia-white with dark eyes, the light sepia being apparently identical in grade with that in ordinary light sepias (c^dc^aF-). An apparent effect on black has been noted only in combinations with the pink-eye factor.

between the red-eyed and albino guinea-pigs. The homozygotes were dirty white at birth, although with dark-red eyes, only slightly less intense than those of normal wild mice. They acquired a more general pale sepia color later in life with especially large amounts of dark pigment in the exposed parts of the skin. They also seem to be entirely lacking in yellow. Finally, CASTLE (1921) has found that the chinchilla variety of rabbit has a fourth allelomorph of albinism, that reduces black to a dark sepia, yellow to white, and, while not affecting the pigment of the iris appreciably, causes sufficient reduction in the retinal pigment to make it relatively easy to obtain a red reflection through the pupil.

In addition to these three albino allelomorphs above the threshold for black, but below that for yellow, and with red eyes, apparently more or less homologous to the red-eyed guinea-pigs, FELDMAN (1922) has described a fourth allelomorph of the mouse (c^r), which seems to be more comparable to factor c^d in guinea-pigs. This variety is described as having dark eyes, a very dark, dull slate color in place of black, and a yellow (in the agouti pattern) intermediate between white and the yellow of wild gray mice. The heterozygotes were paler in color (brownish) and with yellow practically reduced to white.

The albino series of these four rodents may be classified as follows with respect to the thresholds for yellow and black. No exact identification of the genes in the different cases is intended. As DETLEFSEN (1921) has emphasized, such an identification is out of the question. It may perhaps be well to call attention to the fact that c^d and c^r are used in more or less reversed senses in guinea-pigs and mice. Factor c^r in mice, however, seems to give distinctly lighter eyes than C.

TABLE 7

THRESHOLD	FUR COLORS	EYES	GUINEA-PIG	RABBIT	RAT	MOUSE
Yellow.....	Black-red	Black	C c^h	C	C	C
	Sepia-yellow	Black	c^d			c^r
Black.....	Sepia-white	Red	c^r	c^e	c^r	c^d
	Sooty white-white	Pink	c^a	c^h		
	Pure white	Pink		c	c	c

There are cases in other mammals which suggest a threshold difference. PEARSON, NETTLESHIP and USHER (1913) found that the F_2 from a cross between albino Pekingese dogs and black Pomeranians (F_1 being black)

included reds and "lilacs," the latter with albinotic eyes, in addition to the grandparental colors. The case appears to be exactly comparable to the cross between red-eyed white guinea-pigs (c^rc^ree) and blacks ($CCEE$), which produces reds ($C-ee$) and red-eyed sepias (c^rc^rE-) in F_2 in addition to the blacks and red-eyed whites. It would appear that the "albino" Pekingese is really well above the threshold for black, as far as its albino factor is concerned, although below it with respect to red, and that it is a white in appearance because an independent factor tends to replace black with red.

The similarity of the Siamese variety of cat to the Himalayan rabbit was first pointed out by BATESON (1913). These cats are white or nearly so at birth, but later develop considerable brownish pigment, especially on the ears and extremities. No yellow seems to be produced, however. The red pupils (in a favorable light) indicate deficient retinal pigmentation. CASTLE (1922) has obtained data from a breeder, which indicate that the variety is a simple recessive. Dominance of the ordinary intense varieties is not quite complete, however.

The agreement in these six mammals, including those whose genetics has been most exhaustively studied, goes far to prove that a difference in threshold of black and yellow is characteristic of the physiological process affected in albinism, and that the situation described in the guinea-pig is not a mere accident, resting on a few mutations of a polymorphically varying gene.

In attempting to develop further the idea that the albino series affects primarily only one process in pigmentation, the question arises as to whether it is the 15 compounds or the 5 genes which are to be arranged in a linear order of effectiveness with respect to this process.

The first hypothesis implies that the primary products of the activity of the two genes come together before there is any modification of their quantitative relations, while the second implies that such modifications take place before the union of the primary products, and that the results are the same as if the two genes acted on black and yellow pigmentation in entire independence of each other. A third view, that there is reaction with other substances both in a period of separate gene activity and a period of activity of cell products as a whole, would seem more likely than either extreme view. Before considering this compromise hypothesis, however, it will be well to see how far the facts fall into order under the two extreme views.

The possibilities and difficulties of the first hypothesis can be somewhat crudely illustrated by the following scheme. The five genes c^a, c^r, c^d, c^k,

and C are assigned effects in the proportion 0, 1, 3, 4 and 10. If their primary products come together without modification, the effects of the compounds should be in proportion to the sums of the two genic effects. This brings the compounds into the order shown in table 8.

TABLE 8

	HYPOTHETICAL PRIMARY EFFECTS	OBSERVED GRADES		EYE COLOR
		Yellow	Black	
$C-$	10–20	10.6	14.0	Black
$c^k c^k$	8	7.1	13.1	Black
$c^k c^d$	7	7.2	12.4	Black
$c^d c^d$	6	7.0	9.9	Black
$c^k c^r$	5	4.6	13.5	Black
$c^d c^r$	4	4.1	12.0	Black
$c^k c^a$	4	4.6	11.5	Black
$c^d c^a$	3	4.2	7.0	Black
$c^r c^r$	2	0	13.1	Dark red
$c^r c^a$	1	0	8.5	Light red
$c^a c^a$	0	0	0	Pink

The grades of yellow fall into four distinct levels, white (0), cream (4.1 to 4.6), yellow (7.0 to 7.2) and red (10.6); the grades of black rise within each level (of yellow) but fall in the passage from one level to the next (except the last).

The similarity in appearance of the compounds $c^d c^r$ and $c^k c^a$ is explained as due to the identity of the sum of the effects of their combined genes. The scheme thus brings out a certain order among the facts. The levels in intensity of yellow and the drop in intensity of black in the transition from one level to the next require explanation in terms of later reactions. The previously advanced hypothesis that production of yellow interferes with the production of black may be used to explain the second of these phenomena, while the unbroken rise in intensity of black in the eye may be explained as due to the lack of competition with yellow in that region through a higher yellow threshold.

There are, however, rather serious objections to this view, aside from its complexity. It is difficult to formulate any quantitative scheme which can account for the very marked drops in intensity of black in the transitions from $c^r c^r$ to $c^d c^a$ and from $c^k c^r$ to $c^d c^d$. Such a scheme, moreover, leaves it a mere coincidence that each heterozygote is intermediate (or nearly so)

between the corresponding homozygotes and, more generally, that each gene difference has practically the same effect in all cases.

This leads to consideration of the second hypothesis under which each gene has its characteristic effect, primary and secondary as well, on black and yellow, the effects of the compound being merely the sum of the effects of the genes acting independently of each other.

The lines in figure 2 show the intensity of yellow in compounds in which one gene is constant and in which the differences are therefore to be explained as due wholly to the other gene. It will be seen that c^r and c^a are

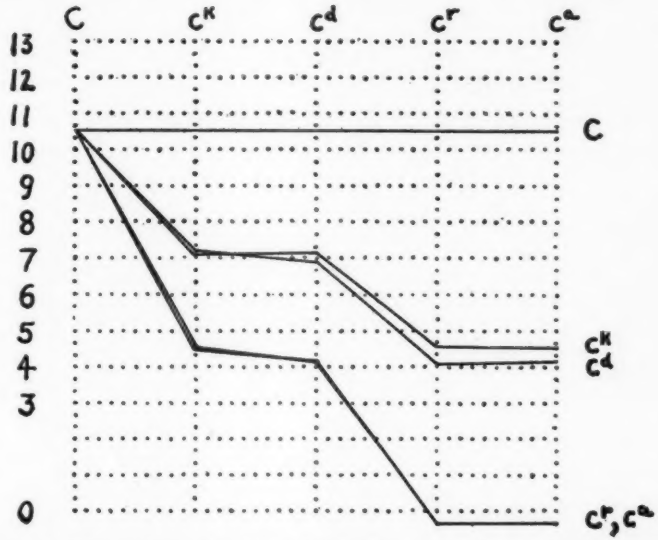

FIGURE 2.—The average grades of intensity of yellow in the albino-series compounds. Each line represents the grade for the compounds in which the factor to the right is combined in succession with each of the factors at the top.

practically identical in effect (or lack of effect) in whatever way they may be combined. Not only is yellow reduced to white in the compounds c^rc^r, c^rc^a and c^ac^a, but $c^dc^r = c^dc^a$ (4.1, 4.2), $c^kc^r = c^kc^a$ (both 4.6). Similarly, c^k and c^d are very close together in effect, with c^k usually giving a little more intensity. Compare c^kc^a with c^dc^a (4.6, 4.2), c^kc^r with c^dc^r (4.6, 4.1), c^kc^k with c^dc^k (7.1, 7.2).

Figure 3 deals similarly with intensity of black. The tendency toward parallelism between the different lines, each representing a series of com-

pounds in which one gene is constant, is obvious. The order, however, is different from that with respect to intensity of yellow.

Disregarding the compounds with the completely dominant intensity factor, there is only one minor exception to the order of effectiveness, c^k, c^r, c^d, c^a. The differences are brought out most strongly in the compounds with c^a ($c^kc^a = 11.5$, $c^rc^a = 8.5$, $c^dc^a = 7.0$, $c^ac^a = 0$). The combinations with c^d give the series $c^kc^d = 12.4$, $c^rc^d = 12.1$, $c^dc^d = 9.9$, $c^ac^d = 7.0$. The combinations with c^r give the series $c^kc^r = 13.5$, $c^rc^r = 13.1$, $c^dc^r = 12.1$ and $c^ac^r = 8.5$. Finally, the combinations with c^k give $c^kc^k = 13.1$, $c^rc^k = 13.5$, $c^dc^k = 12.4$, and $c^ac^k = 11.5$.

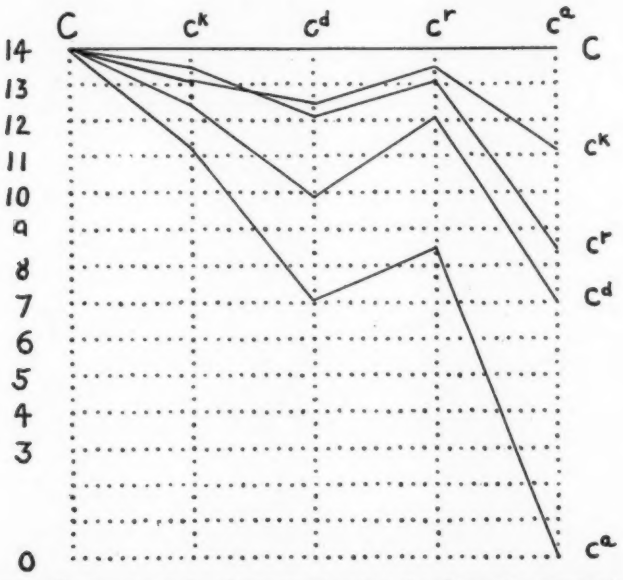

FIGURE 3.—The average grades of intensity of sepia in the albino-series compounds. Each line represents the grade for the compounds in which the factor to the right is combined in succession with each of the factors at the top.

The doubled effects of the genes on both yellow and black are shown in the series of homozygotes in figure 4. The order of the genic effects is the same as in figures 2 and 3.

As pointed out previously, the agreements in these series are mere coincidences on the first hypothesis. This seems too much to assign to coincidence. It can thus hardly be doubted that the genes act in independence

of each other to at least a considerable extent. On the other hand, there are irregularities which indicate that there is not complete independence.

As c^a is below the threshold for yellow and nearly so for black, the lowest lines in figures 2 and 3 (repeated in figure 5) should represent the effects of the five single genes, the lines in figure 4 representing the doubled effects of the same genes. Under completely independent activity of the two genes in a compound, the homozygotes (figure 4) should produce exactly

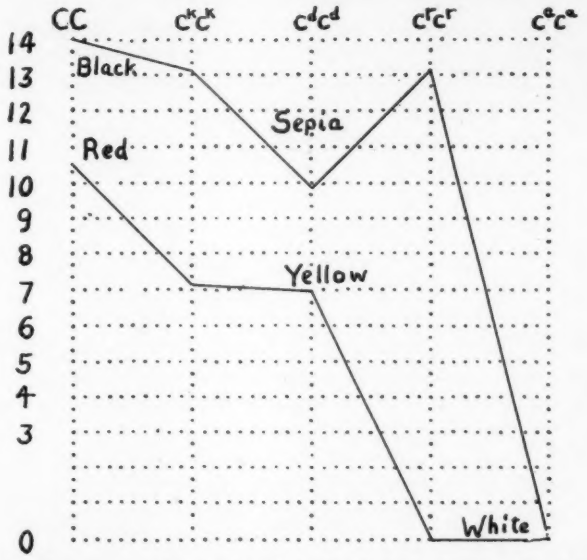

FIGURE 4.—The average grades of sepia and of yellow in the five homozygotes of the albino series.

twice the amount of pigment as the heterozygotes with albinism. The different factors should contribute fixed amounts in every compound in which they enter. Unfortunately, the scale used for measuring intensity can not be considered sufficiently close to a quantitative one to enable final conclusions to be drawn as to how far the data meet these conditions. As already pointed out, it is certain that smaller differences in the absolute amount of pigment are recognizable in the light sepias than in the dark sepias, with the consequence that the scale needs stretching in the upper part relative to the lower. In spite of the unsatisfactory character of the scale in this connection, there are certain points which indicate that the action of the genes is not wholly independent. In the first place, the com-

plete dominance of factor *C* can hardly be a mere question of imperfection of the scale, at least as regards red. Most intense reds, whether homozygous *CC* or heterozygous with albinism Cc^a, are of grades 10 and 11. This is well below the limit of intensity (grade 13) found regularly in a particular inbred family. Thus, it can hardly be maintained that there is twice as much pigment in *CC* as in Cc^a. There probably are limiting factors in intensity of pigmentation independent of the albino series which are responsible for the complete dominance of factor *C*.

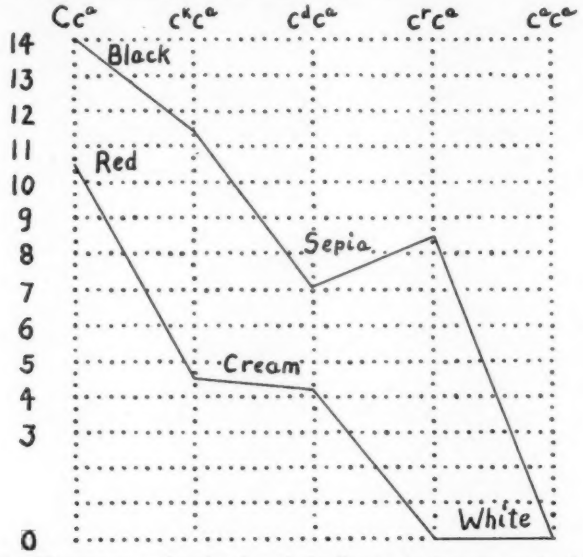

FIGURE 5.—The average grades of sepia and of yellow in the five compounds with albinism of the albino series.

Aside from the dominance of *C*, the most serious departure from expectation on the basis of independent activity of the genes comes in the effect of factor c^r, which, in combination with c^a, seems decidedly more like c^d than c^k in effect on black, although in other combinations it approaches very closely to c^k in effect, or even rises above it. However, the entire process of pigment production is hardly likely to be localized in the immediate vicinity of the two chromosomes carrying the albino factor. The surprising thing is that the effects of the compounds agree as well as they do with the hypothesis that the genes act independently on pigment production, or at least that the most important modifications of their effects takes place before the separate identity of their products is lost.

The problem thus reduces in the main to the explanation of the different effects of the five genes on black and yellow in fur and skin and on eye color.

Figures 4 and 5 suggest a rising trend in effect on pigmentation in the series c^a, c^r, c^d, c^k and C, but a tendency toward negative correlation between black and yellow in their deviations from this trend. The evidence for different thresholds for yellow and black, as responsible for the peculiar effects of c^r,—rather intense black, no yellow,—has already been discussed. This threshold difference is one which must be traced back to the separate activities of the genes. The rates of production of the primary products of factors c^r and c^a (on the view adopted) appear to be below the threshold for yellow, with the consequence that these genes contribute nothing to intensity of yellow in any compound in which they enter.

The drop in intensity of black with c^d as compared with c^r in all compounds accompanying the first appearance of the power to produce yellow, suggests some sort of physical antagonism between the processes of black and yellow pigmentation, perhaps competition for some other substance. The absence of any such drop in the intensity of black in the eye (c^d, black eye; c^r, red eye) requires the further hypothesis that this interference with black production by yellow is absent in the eye, perhaps because the threshold for yellow is never passed in this location.

The hypotheses suggested to account for the irregularities in the effects of the albino series, namely, the threshold difference between black and yellow, the antagonistic action of yellow on black above the threshold of the former, and the difference in threshold for yellow in the eye and skin, are the same as those previously advanced. It is suggested here, however, that they apply to the primary products of the genes instead of to the compounds.

ALBINISM AND DILUTION IN OTHER ANIMALS

Albinism is one of the commonest types of color variation among all sorts of animals which have melanin pigmentation. How far is it safe to identify the albinism of different species physiologically, and how far genetically? In the first place, all the piebalds, roans and dominant whites must be eliminated from consideration. They are doubtless as distinct from true albinism, physiologically, as experiments with the laboratory rodents have shown them to be, genetically. There remain, however, numerous pink-eyed, red-eyed, perhaps even black-eyed, whites, reported in all classes of vertebrates, which may be truly homologous (HAECKER 1918, DUNN 1921). The genetical studies indicate that true

incomplete albinism is to be looked for in varieties in which both black and yellow are reduced in intensity, the latter more drastically. Dilution of black alone or of yellow alone, when both colors are present, may be rejected. Moreover, not all simultaneous dilution of black and yellow is related to albinism. The type of dilution in which black is reduced to a maltese color, and yellow to cream, as found in blue mice and rabbits and in maltese cats, has been shown in all three of these cases to be transmitted independently of albinism. In albino-series dilution, black seems always to be reduced to a brown color resembling human brown hair.

It is a remarkable fact that only one series of factors answering the above description has been found in each of the four laboratory rodents. This is not because of the rarity of mutations, as multiple allelomorphs of albinism have been found in each case. At least two were first found in animals caught wild. There is a strong indication here that just one physiological process, interference with which can lead at a single step to albinism, is involved in each case, and that in each case this is controlled primarily by just one gene.

There is direct genetic evidence tending to connect albino factors in three species. Albinism in the rat is linked very closely with "red-eyed yellow" and less closely with "pink-eyed yellow," two varieties in which black is greatly reduced in intensity, but yellow is unaffected (CASTLE 1916, 1919, DUNN 1920). Albinism in the mouse is also linked, but not very closely, with a pink-eyed variation closely resembling that of the rat (HALDANE, SPRUNT and HALDANE 1915, CASTLE 1919, DUNN 1920). Complete albinism in the wood mouse, *Peromyscus maniculatus*, is closely linked with "pallid," a variation closely resembling red-eyed yellow of rats (SUMNER 1922). In the guinea-pig, it is true, albinism seems to be wholly independent of a variation (*p*) resembling pink-eyed yellow of rats and mice. It is asking a good deal of the chromosomes, however, to expect them to maintain their identity in the enormous period since the separation of the hystricomorph and murimorph rodents.

No other mammals have been investigated with sufficient thoroughness to give evidence as to whether more than one apparent albino series occurs within the same species. Albinism of apparently the same kind as in those cited above is, however, very widespread. In the human species, albinism is, of course, well known. Unfortunately, there seems to be much confusion in the literature with types of dilution of color of entirely different kinds. The researches of PEARSON, NETTLESHIP and USHER (1913) indicate that human albinos often have considerable brown pigment. They also, however, describe albinos with yellow or even red in the hair, but no brown.

These seem to be more comparable to the genetically unrelated red-eyed and pink-eyed yellows mentioned above, in which a factor which specifically reduces black pigment is involved. It seems clear that such dilute variations as the yellowish-haired, hazel-eyed "White Indians" of Darien discovered recently by the Marsh expedition and which the writer has had the opportunity of observing, have nothing to do with albinism as the term is understood in the laboratory rodents. If an albino allelomorph is responsible for the paleness of the yellow (as contrasted with red) in these White Indians, the same factor must also be present in the normally-colored brown Indians from whom they segregate, if the analogy with rodent albinism is carried out.

Among horses, WRIEDT (1918) finds that albinism (white with glass eye) is incompletely recessive to the intense colors, such as black, bay and chestnut. In the heterozygotes red or yellow pigmentation is reduced to a pale-cream, but black is not appreciably modified. There is thus indication of a more drastic dilution of red than of black. There are more or less similar dilute variations and also albinos in cattle, but the mode of inheritance has not been satisfactorily worked out.

Albinos with or without pink eyes are relatively common among birds. Perhaps the most interesting possible parallel to the series in rodents is that in the ring-doves. The white ring-dove, with only traces of brownish pigment in a half ring on the neck and with deficient pigmentation of the eyes, is a sex-linked recessive to the blond variety (*Streptopelia risoria*). The latter has a black half ring on the neck and sufficient brown pigment elsewhere in the plumage to give a pale fawn color and dark eyes (STRONG 1912, WHITMAN and RIDDLE 1919). WHITMAN made additional crosses involving a number of much more intensely colored wild species. There is clear evidence in certain of these crosses (as with *Streptopelia humilis* and *Turtur orientalis*) that white is a sex-linked recessive to the dark color. This might be the same sex-linked difference as that by which white differs from blond. Appropriate crosses indicated, however, that blond also is a sex-linked recessive to dark color. While the authors do not express their results in the Mendelian terminology, the simplest interpretation which is in harmony with the data (with one apparent exception) is that intense, blond and white form a series of triple allelomorphs. There is also a sex-linked pair of factors in pigeons,—dominant intensity of blacks, blues and reds as opposed to dilution of duns, silvers and yellows (COLE 1912), which has some similarity with the albino series of mammals. Whether there is any real homology between the dove and pigeon series or between either and albinism, it is too early to say.

Among lower vertebrates, HAECKER (1918) has shown that an incomplete albino of the salamander, *Ambystoma tigrinum*, is imperfectly recessive to the normal variety. These albinos had grayish areas in the skin, containing both black and yellow melanophores, and also had pigment in the iris, but red pupils, owing to deficient retinal pigmentation. WHITING (1919) has described two interesting tadpoles of the green frog (*Rana clamitans*). In one, yellow seemed entirely lacking, black was reduced to a very light sepia, but both iris and pupil were dark. The other was yellow with very little if any black, and with golden iris and pink pupil. The former might well be comparable to rodent albinism, the latter certainly was not. AIDA (1921) has investigated the genetics of a number of varieties of the fish, *Aplocheilus latipes*. One recessive factor reduces black to blue black. The same factor reduces red to white. There is thus some resemblance to the working of factor c^r in guinea-pigs.

The following general conclusions as regards homologies in different species seem warranted: Disturbances in melanin pigmentation which *may* be homologous to guinea-pig albinism, are relatively common throughout the vertebrate phylum. Certain of the peculiarities of the guinea-pig series of allelomorphs, a particular type of dilution of black associated with a more drastic dilution of yellow and occurring in eyes as well as skin, are found widely distributed as the effects of a more or less completely recessive unit-factor variation. In the mammals most intensively studied there is a rather strong indication that there is only one process liable to such an effect, and that this is controlled essentially by only one gene.

SUMMARY

As the writer may have gone into speculation at some points to a greater extent than the reader may think warranted, it will be well to distinguish carefully in the summary what is fact and what is speculation.

The existence of at least five allelomorphs in the albino series of guinea-pigs, C, c^k, c^d, c^r and c^a, the writer wishes to present as the simplest description of the genetic facts. The average grades of intensity of the 15 compounds of these factors, with respect to black and yellow pigmentation of the fur and black in the eyes, are also presented as facts within the limits indicated by the probable errors. It is desired to call attention to the fact that the order of intensity of the compounds with respect to black in the fur is unmistakably different from the order with respect to yellow in the fur or black in the eyes.

Certain speculations are presented in the attempt to find order in the grades of black and yellow in the fur and black in the eye. It is found

that the compounds are, in the main, such as would result if each of the two genes in the zygote affect pigment production independently. The relative effects of the genes on yellow (in the order c^a, c^r, c^d, c^k and C) are best illustrated by the grades of intensity of the compounds of each with albinism, namely, 0.0, 0.0, 4.1, 4.6 and 10.6, respectively. The relative effects on black may be illustrated by the sepia grades of the same compounds, namely, 0.0, 8.5, 7.5, 11.5 and 14.0, respectively. The relative effects on eye color may be indicated by the qualitative terms, pink, light red and black, for the last three.

There is complete dominance of the intensity factor C over all of the others, suggesting that in these compounds some factor outside of the albino series plays the rôle of a limiting factor.

It is suggested that the factors of the albino series determine the rate of some one process fundamental to all pigmentation and that the irregularities in the order of effect on different kinds of pigment, or in different regions of the body, are due to subsequent physiological processes with which the albino series of genes has nothing to do. Among such processes one which determines a higher threshold for yellow than for black finds extensive corroboration in the albino series of other mammals. A tendency for the production of yellow to interfere with the production of black is suggested by the guinea-pig series. The differences between intensity of black in the fur and the eye suggest that competition from yellow is lacking in the eye, which thus shows more simply than the fur the effects of the different genes on intensity of black.

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APPENDIX—TABLES 9 to 21

TABLE 9

The intensity of sepia among black-eyed and red-eyed dilutes of different genetic constitutions.

GENETIC CONSTITUTION	CRITERION*	GRADE OF SEPIA												NUMBER	MEAN
		3	4	5	6	7	8	9	10	11	12	13	14		
$c^k c^k$	A	..	..	..	..	..	..	..	..	..	..	1	1	2	13.50±.35
	B	..	..	..	..	..	..	..	..	..	4	6	5	15	13.07±.13
	C	..	..	..	..	..	..	..	..	..	3	12	5	20	13.10±.11
	D	..	..	..	..	..	..	..	..	..	3	5	4	12	13.08±.14
$c^k c^d$	A	..	..	..	..	..	..	..	1	..	1	..	..	2	11.00±.36
	B	..	..	..	..	..	..	..	..	1	10	12	..	23	12.48±.11
	C	..	..	..	..	..	..	..	..	..	..	..	1	1	14.00±.51
	D	..	..	..	..	..	..	..	..	..	1	1	..	2	12.50±.36
$c^k c^r$	A	..	..	..	..	..	..	..	..	..	..	..	..	..	.....
	B	..	..	..	..	..	..	..	..	..	6	10	33	49	13.55±.07
	C	..	..	..	..	..	..	..	..	1	2	5	8	16	13.25±.12
	D	..	..	..	..	..	..	..	..	..	..	5	2	7	13.29±.18
$c^k c^a$	A	..	..	..	..	..	..	..	13	31	46	11	..	101	11.54±.05
	B	..	..	..	..	..	..	..	12	32	53	10	..	107	11.57±.05
	C	..	..	..	..	..	..	..	1	14	6	1	..	22	11.32±.11
	D	..	..	..	..	..	..	..	1	7	5	1	..	14	11.43±.14
$c^d c^d$	A	..	..	..	..	..	4	20	4	14	..	..	..	42	9.67±.14
	B	..	..	..	2	..	5	9	13	7	9	1	..	46	10.02±.14
	C	..	..	..	..	..	..	..	..	..	..	..	..	..	.....
	D	..	..	..	..	..	..	2	1	2	1	..	..	6	10.33±.38
$c^d c^r$	A	..	..	..	..	..	..	..	..	3	20	8	..	31	12.16±.10
	B	..	..	..	..	..	1	..	3	12	22	29	..	67	12.10±.07
	C	..	..	..	..	..	..	..	..	3	15	9	..	27	12.22±.11
	D	..	..	..	..	..	..	..	..	7	2	1	..	10	11.40±.18
$c^d c^a$	A	1	3	10	28	43	48	6	1	..	..	..	..	140	7.04±.06
	B	..	..	13	28	40	29	9	..	..	..	..	..	119	6.94±.06
	C	..	..	1	1	8	7	2	..	..	..	..	..	19	7.42±.16
	D	..	..	..	1	..	..	..	..	..	..	..	..	1	6.00±.71
$c^r c^r$	A	..	..	..	..	..	..	..	..	..	3	21	10	34	13.21±.10
	B	..	..	..	..	..	..	1	..	2	4	11	10	28	12.93±.11
	C	..	..	..	..	..	..	..	..	..	1	3	2	6	13.17±.24
$c^r c^a$	A	1	..	..	5	10	25	12	5	7	6	..	..	71	8.59±.12
	B	..	..	..	1	11	15	12	1	2	..	..	..	42	8.17±.16
	C	..	..	..	..	5	10	6	3	3	1	..	..	28	8.70±.19

* Groups A and B include all in experiments J and K through 1923 (with the exceptions noted in the text). Group A includes those from matings which could only produce the type of black-

eyed or red-eyed dilute designated. Group B includes all other graded sepias in these experiments (compare tables 13 to 20). The grade of yellow was the principal criterion in distinguishing classes c^kc^k, c^kc^d, and c^dc^d with yellow of grades 7 and 8, from classes c^kc^r, c^kc^a, c^dc^r, and c^dc^a with cream of grades 3, 4 and 5). The grade of sepia and the expected ratio were used when necessary, however. Group C includes all of definitely known constitution from experiments L, N and UR during the same period. Group D includes sepias from L, N and UR which produced two or more types of black-eyed dilutes and for which the grade of yellow was used as a criterion for separation.

TABLE 10

The intensity of yellow among intense and dilute young of different genetic constitutions.

GENETIC CONSTITUTION	CRITERION*	GRADE OF YELLOW											NUMBER	MEAN
		3	4	5	6	7	8	9	10	11	12	13		
CC	A	..	..	..	..	..	..	..	.†	..	..	.†	..	.....
Cc^k	A	..	..	..	..	..	..	..	5	8	2	..	15	10.80±.11
Cc^d	A	..	..	..	..	..	..	1	18	2	..	..	21	10.05±.09
Cc^r	A	..	..	..	..	..	..	..	..	..	..	..	..	.....
Cc^a	A	..	..	..	..	..	..	2	23	14	..	..	39	10.31±.07
$C-$	B	..	..	..	..	..	..	1	66	83	13	1	164	10.68±.03
c^kc^k	A	..	..	..	..	5	..	..	..	..	..	..	5	7.00±.10
	B	..	..	..	..	14	3	..	..	..	..	..	17	7.18±.05
	C	..	..	..	1	16	2	..	..	..	..	..	19	7.05±.05
c^kc^d	A	..	..	..	..	1	1	..	..	..	..	..	2	7.50±.20
	B	..	..	..	..	23	3	..	..	..	..	..	26	7.12±.06
	C	..	..	..	..	..	1	..	..	..	..	..	1	8.00±.34
c^kc^r	A	..	..	..	..	..	..	..	..	..	..	..	..	.....
	B	1	12	25	1	..	..	..	..	..	..	..	39	4.67±.07
	C	1	8	6	2	..	..	..	..	..	..	..	17	4.53±.10
c^kc^a	A	2	49	33	8	..	..	..	..	..	..	..	92	4.51±.05
	B	..	34	35	11	2	..	..	..	..	..	..	82	4.77±.05
	C	..	17	3	1	..	..	..	..	..	..	..	21	4.24±.11
c^dc^d	A	..	..	..	3	32	7	..	..	..	..	..	42	7.10±.06
	B	..	..	2	10	45	7	..	..	..	..	..	64	6.89±.05
	C	..	..	..	..	..	..	..	..	..	..	..	..	.....
c^dc^r	A	..	33	2	..	..	..	..	..	..	..	..	35	4.06±.04
	B	5	48	10	..	..	..	..	..	..	..	..	63	4.08±.03
	C	..	24	3	..	..	..	..	..	..	..	..	27	4.11±.05
c^dc^a	A	3	91	25	..	..	..	..	..	..	..	..	119	4.18±.03
	B	7	94	20	2	..	..	..	..	..	..	..	123	4.14±.03
	C	..	14	2	..	..	..	..	..	..	..	..	16	4.13±.08

* The groups A, B and C have the same significance as in table 9. Groups A and C include young whose constitution is uniquely determined from their ancestry, from experiments J and K and from L, N and UR, respectively. Group B includes all other graded yellows from experiments J and K assigned on the basis of both grade of yellow and sepia and of expected ratio of classes.

† Inbred family 2 is regularly graded 10, while family 32 is graded 13. Both are *CC*.

TABLE 11

The intensity of sepia in all compounds of the albino series. The figures are the sums of the separate groups (A, B, C and D) as given in table 9.

GENETIC CONSTITUTION	WHITE	GRADE OF SEPIA												NUMBER	MEAN	σ
		Light				Medium			Dark			Black				
	0	3	4	5	6	7	8	9	10	11	12	13	14			
$C-$	..	..	..	..	..	..	..	..	..	..	..	..	x	...	14.00	...
$c^k c^k$	..	..	..	..	..	..	..	..	..	..	10	24	15	49	13.10± .07	0.74
$c^k c^d$	..	..	..	..	..	..	..	..	1	1	12	13	1	28	12.43± .10	0.75
$c^k c^r$	..	..	..	..	..	..	..	..	..	1	8	20	43	72	13.46± .06	0.71
$c^k c^a$	..	..	..	..	..	..	..	..	27	84	110	23	..	244	11.53± .03	0.79
$c^d c^d$	..	..	..	..	2	..	9	31	18	23	10	1	..	94	9.88± .09	1.36
$c^d c^r$	..	..	..	..	..	..	1	..	3	25	59	47	..	135	12.09± .05	0.84
$c^d c^a$	..	1	3	24	58	91	84	17	1	..	..	..	..	279	7.02± .04	1.05
$c^r c^r$	..	..	..	..	..	..	..	1	..	2	8	35	22	68	13.09± .07	0.86
$c^r c^a$	..	1	..	..	6	26	50	30	9	12	7	..	..	141	8.49± .09	1.52
$c^a c^a$	x	..	..	..	..	..	..	..	..	..	..	..	..	..	0.00	...

TABLE 12

The intensity of yellow in all compounds of the albino series. The figures are the sums of the separate groups (A, B and C) as given in table 10.

	GRADE OF YELLOW												NUMBER	MEAN	σ
	White	Cream			Yellow			Red							
	0	3	4	5	6	7	8	9	10	11	12	13			
$C-$	..	..	..	..	..	..	..	4	112	107	15	1	239	10.57± .03	0.64
$c^k c^k$	..	..	..	..	1	35	5	..	..	..	..	..	41	7.10± .03	0.32
$c^k c^d$	..	..	..	..	..	24	5	..	..	..	..	..	29	7.17± .05	0.42
$c^k c^r$	..	2	20	31	3	..	..	..	..	..	..	..	56	4.63± .05	0.61
$c^k c^a$	..	2	100	71	20	2	..	..	..	..	..	..	195	4.59± .04	0.73
$c^d c^d$	..	..	..	2	13	77	14	..	..	..	..	..	106	6.97± .04	0.59
$c^d c^r$	..	5	105	15	..	..	..	..	..	..	..	..	125	4.08± .02	0.39
$c^d c^a$	..	10	199	47	2	..	..	..	..	..	..	..	258	4.16± .02	0.47
$c^r c^r$	x	..	..	..	..	..	..	..	..	..	..	..	..	0	0
$c^r c^a$	x	..	..	..	..	..	..	..	..	..	..	..	..	0	0
$c^a c^a$	x	..	..	..	..	..	..	..	..	..	..	..	..	0	0

TABLES 13 to 20.—These tables give the results of all matings in experiments J and K through 1923 (with the exceptions noted in the test). All young are included with the few exceptions noted below each table. The young are assigned to the expected classes on the basis of sepia and yellow, and eye color. The grade of yellow is the primary criterion where more than one class of young is expected. Compounds c^bc^b, c^bc^d and c^dc^d with yellow of grades 7 to 8 being separated from c^bc^r, c^bc^a, c^dc^r, and c^dc^a with cream of grades 3 to 5. Within these groups of compounds the grade of sepia is used as a criterion. Thus, c^dc^a is separated from c^bc^r, c^bc^a or c^dc^r as of grade 9 or less, the latter classes being considered as of grade 10 or more. The separation of c^bc^r (grade 13 or 14) from c^bc^a or c^dc^r (grades 10 to 12) where both should be produced, is less satisfactory. In the few cases in which both c^bc^a and c^dc^r should be produced, these are assigned merely by expected ratio. There were no matings which produced more than one of the varieties with yellow (c^bc^b, c^bc^d, c^dc^d). Where both kinds of red-eyed dilutes were expected (c^rc^r and c^rc^a), the contrast in eye color and grade of sepia within the litter was used as far as possible. In a few cases it was necessary to draw an arbitrary line between grades 11 and 12 to separate them. Young were only assigned classes possible from their ancestry. The range of variation in each compound which this necessitated may be seen by a study of groups A and B in tables 9 and 10, since all graded young included in tables 13 to 20 are there included.

TABLE 13

The results of the matings in experiments J and K between albinos (c^ac^a) and each of the compounds of the albino series. It may be added that matings of type $CC\times c^ac^a$ have been made in other experiments and have produced only intense young (Cc^a). Matings of type $Cc^r\times c^ac^a$ have also been made in other experiments and have produced the two expected classes, intense (Cc^a) and light sepias with red eyes (c^rc^a). Matings of albino by albino have produced only albino young.

PARENTS	NUMBER OF MATINGS	GENETIC CONSTITUTION OF OFFSPRING											TOTAL
		$C-$	c^bc^b	c^bc^d	c^bc^r	c^bc^a	c^dc^d	c^dc^r	c^dc^a	c^rc^r	c^rc^a	c^ac^a	
$CC\times c^ac^a$	..	x	..	..	..	..	..	..	..	..	..	..	x
$Cc^b\times c^ac^a$	3	15	..	..	..	19	..	..	..	..	..	..	34*
$Cc^d\times c^ac^a$	2	13	..	..	..	..	..	..	8	..	..	..	21
$Cc^r\times c^ac^a$	..	x	..	..	..	..	..	..	..	..	x	..	x
$Cc^a\times c^ac^a$	5	30	..	..	..	..	..	..	..	..	..	43	73
$c^bc^b\times c^ac^a$	5	..	..	..	..	18	..	..	..	..	..	..	18
$c^bc^d\times c^ac^a$	8	..	..	..	..	32	..	..	40	..	..	..	72†
$c^bc^r\times c^ac^a$	5	..	..	..	..	23	..	..	..	..	21	..	44
$c^bc^a\times c^ac^a$	11	..	..	..	..	85	..	..	..	..	..	77	162
$c^dc^d\times c^ac^a$	6	..	..	..	..	..	..	..	67	..	..	..	67
$c^dc^r\times c^ac^a$	3	..	..	..	..	..	..	..	11	..	8	..	19
$c^dc^a\times c^ac^a$	21	..	..	..	..	..	..	..	87	..	..	105	192
$c^rc^r\times c^ac^a$	1	..	..	..	..	..	..	..	..	..	4	..	4
$c^rc^a\times c^ac^a$	1	..	..	..	..	..	..	..	..	..	2	1	3
$c^ac^a\times c^ac^a$	1	..	..	..	..	..	..	..	..	..	..	3	3

* Two black-eyed whites (either Cc^a or c^bc^a) omitted.

† 29 with cream but no sepia (equally likely to be c^bc^a or c^dc^a) omitted.

TABLE 14

The results of the matings in experiments J and K between heterozygous red-eyed dilute ($c^r c^a$) and compounds in the albino series (except the matings included with an albino) included in table 13.

PARENTS	NUMBER OF MATINGS	GENETIC CONSTITUTION OF OFFSPRING											TOTAL
		$C-$	$c^k c^k$	$c^k c^d$	$c^k c^r$	$c^k c^a$	$c^d c^d$	$c^d c^r$	$c^d c^a$	$c^r c^r$	$c^r c^a$	$c^a c^a$	
$CC \times c^r c^a$	x	..	..	..	..	..	..	..	..	..	..	..	..
$Cc^k \times c^r c^a$	2	12	..	..	12	17	..	..	..	..	..	..	41*
$Cc^d \times c^r c^a$	4	27	..	..	..	..	..	11	17	..	..	..	55†
$Cc^r \times c^r c^a$	x	..	..	..	..	..	..	..	..	..	..	..	..
$Cc^a \times c^r c^a$	2	18	..	..	..	..	..	..	..	..	6	10	34
$c^k c^k \times c^r c^a$	1	..	..	..	5	15	..	..	..	..	..	..	20‡
$c^k c^d \times c^r c^a$	x	..	..	..	..	..	..	..	..	..	..	..	..
$c^k c^r \times c^r c^a$	1	..	..	..	4	3	..	..	..	2	2	..	11+
$c^k c^a \times c^r c^a$	7	..	..	..	19	18	..	..	..	..	16	13	66§
$c^d c^d \times c^r c^a$	1	..	..	..	..	..	..	4	5	..	..	..	9¶
$c^d c^r \times c^r c^a$	2	..	..	..	..	..	..	3	2	3	1	..	9
$c^d c^a \times c^r c^a$	5	..	..	..	..	..	..	10	15	..	13	13	51**
$c^r c^r \times c^r c^a$	1	..	..	..	..	..	..	..	..	1	1	..	2
$c^r c^a \times c^r c^a$	3	..	..	..	..	..	..	..	..	26	50	20	96

* 7 with cream only (grades 4, 5) assigned 4 to $c^k c^r$ and 3 to $c^k c^a$.
† 10 with cream only (grade 4, 5) assigned 5 to $c^d c^r$ and 5 to $c^d c^a$.
‡ 2 with cream only (grade 4) either $c^k c^r$ or $c^k c^a$ omitted.
§ 2 with cream only (grades 4, 5) assigned 1 to $c^k c^r$ and 1 to $c^k c^a$.
+ 10 with cream only (1 grade 6, 6 grade 4, 3 ungraded) assigned 5 to $c^k c^r$ and 5 to $c^k c^a$.
¶ 6 with cream only omitted.
** 1 with cream only assigned to $c^d c^r$ (might equally well be $c^d c^a$).

TABLE 15

The results of the matings in experiments J and K in which one of the parents was a homozygous red-eyed dilute ($c^r c^r$) and which are not included in previous tables.

PARENTS	NUMBER OF MATINGS	GENETIC CONSTITUTION OF OFFSPRING											TOTAL
		$C-$	$c^k c^k$	$c^k c^d$	$c^k c^r$	$c^k c^a$	$c^d c^d$	$c^d c^r$	$c^d c^a$	$c^r c^r$	$c^r c^a$	$c^a c^a$	
$c^k c^d \times c^r c^r$	2	..	..	..	7	..	..	6	..	..	..	..	13*
$c^d c^d \times c^r c^r$	3	..	..	..	..	..	..	23	..	..	..	..	23
$c^d c^r \times c^r c^r$	3	..	..	..	..	..	..	20	..	14	..	..	34†
$c^d c^a \times c^r c^r$	2	..	..	..	..	..	..	8	..	..	12	..	20
$c^r c^r \times c^r c^r$	3	..	..	..	..	..	..	..	..	18	..	..	18

* 4 ungraded black-and-cream tortoise-shells (either $c^k c^r$ or $c^d c^r$) omitted.
† 9 of uncertain eye color and without cream or white tortoise-shell markings in fur omitted (either $c^d c^r$ or $c^r c^r$).

TABLE 16

The results of the matings in experiments J and K in which one of the parents was a light dilute carrying albinism ($c^d c^a$) and which are not included in previous tables.

PARENTS	NUMBER OF MATINGS	GENETIC CONSTITUTION OF OFFSPRING											TOTAL
		$C-$	$c^k c^k$	$c^k c^d$	$c^k c^r$	$c^k c^a$	$c^d c^d$	$c^d c^r$	$c^d c^a$	$c^r c^r$	$c^r c^a$	$c^a c^a$	
$CC \times c^d c^a$	2	7	..	..	..	..	..	..	..	..	..	..	7
$Cc^d \times c^d c^a$	1	3	..	..	..	..	5	..	5	..	..	..	13
$Cc^r \times c^d c^a$	1	5	..	..	..	..	..	3	..	..	4	..	12
$c^k c^k \times c^d c^a$	1	..	..	7	..	9	..	..	..	..	..	..	16
$c^k c^r \times c^d c^a$	1	..	..	2	..	2	..	2	..	..	5	..	11*
$c^k c^a \times c^d c^a$	4	..	..	18	..	20	..	..	13	..	..	10	61
$c^d c^d \times c^d c^a$	1	..	..	..	..	..	1	..	2	..	..	..	3
$c^d c^r \times c^d c^a$	2	..	..	..	..	..	3	7	4	..	6	..	20†
$c^d c^a \times c^d c^a$	8	..	..	..	..	..	37	..	78	..	..	24	139

* 4 dark sepia-cream, divided equally between $c^k c^a$ and $c^d c^r$.
† 1 with cream only (either $c^d c^r$ or $c^d c^a$) assigned to $c^d c^a$.

TABLE 17

The results of the matings in experiments J and K in which one of the parents was a light dilute carrying red-eye ($c^d c^r$), and which are not included in previous tables.

PARENTS	NUMBER OF MATINGS	GENETIC CONSTITUTION OF OFFSPRING											TOTAL
		$C-$	$c^k c^k$	$c^k c^d$	$c^k c^r$	$c^k c^a$	$c^d c^d$	$c^d c^r$	$c^d c^a$	$c^r c^r$	$c^r c^a$	$c^a c^a$	
$CC \times c^d c^r$	1	6	..	..	..	..	..	..	..	..	..	..	6
$Cc^d \times c^d c^r$	1	..	..	..	..	..	..	1	..	..	..	..	1
$c^k c^a \times c^d c^r$	1	..	..	4	5	..	..	..	6	..	5	..	20*
$c^d c^d \times c^d c^r$	6	..	..	..	..	..	25	33	..	..	..	..	58†
$c^d c^r \times c^d c^r$	6	..	..	..	..	..	18	38	..	21	..	..	77

* 1 cream (either $c^k c^r$ or $c^d c^a$) assigned to $c^d c^a$.
† 10 sepias (grades 9 to 12) divided equally between $c^d c^d$ and $c^d c^r$.

TABLE 18

The results of the matings in experiments J and K in which one of the parents was a homozygous light dilute ($c^d c^d$) and which are not included in previous tables.

PARENTS	NUMBER OF MATINGS	GENETIC CONSTITUTION OF OFFSPRING											TOTAL
		$C-$	$c^k c^k$	$c^k c^d$	$c^k c^r$	$c^k c^a$	$c^d c^d$	$c^d c^r$	$c^d c^a$	$c^r c^r$	$c^r c^a$	$c^a c^a$	
$CC \times c^d c^d$	3	22	..	..	..	..	..	..	..	..	..	..	22
$Cc^a \times c^d c^d$	1	23	..	..	..	..	..	..	15	..	..	..	38
$c^k c^a \times c^d c^d$	1	..	..	6	..	..	..	..	6	..	..	..	12
$c^d c^d \times c^d c^d$	8	..	..	..	..	..	65	..	.	..	..	..	65

TABLE 19

The results of the matings in experiments J and K in which one of the parents was a dark dilute (c^kc^a, c^kc^r or c^kc^k) and which are not included in previous tables.

PARENTS	NUMBER OF MATINGS	GENETIC CONSTITUTION OF OFFSPRING											TOTAL
		$C-$	c^kc^k	c^kc^d	c^kc^r	c^kc^a	c^dc^d	c^dc^r	c^dc^a	c^rc^r	c^rc^a	c^ac^a	
$CC\times c^kc^a$	3	40	..	..	..	..	..	..	..	..	..	..	40
$Cc^r\times c^kc^a$	1	4	..	..	4	..	..	..	..	..	0	..	8
$Cc^a\times c^kc^a$	3	11	..	..	..	4	..	..	..	..	..	9	24
$c^kc^k\times c^kc^a$	1	..	1	..	..	4	..	..	..	..	..	..	5
$c^kc^a\times c^kc^a$	6	..	20	..	..	30	..	..	..	..	..	19	69*
$c^kc^k\times c^kc^r$	1	..	5	..	2	..	..	..	..	..	..	..	7†
$c^kc^r\times c^kc^r$	2	..	1	..	3	..	..	..	..	2	..	..	6‡
$CC\times c^kc^k$	1	14	..	..	..	..	..	..	..	..	..	..	14
$Cc^d\times c^kc^k$	1	6	..	2	..	..	..	..	..	..	..	..	8
$Cc^a\times c^kc^k$	1	7	..	..	..	5	..	..	..	..	..	..	12

* A black-eyed white (either c^kc^k or c^kc^a) assigned to c^kc^a.

† 9 blacks (4 grade 14, 4 grade 13, 1 ungraded) omitted.

‡ 8 blacks (3 grade 14, 4 grade 13, 1 grade 12, eye colors uncertain) omitted.

TABLE 20

The results of the matings in experiments J and K between intense animals ($C-\times C-$).

PARENTS	NUMBER OF MATINGS	GENETIC CONSTITUTION OF OFFSPRING											TOTAL
		$C-$	c^kc^k	c^kc^d	c^kc^r	c^kc^a	c^dc^d	c^dc^r	c^dc^a	c^rc^r	c^rc^a	c^ac^a	
$Cc^a\times Cc^a$	2	28	..	..	..	..	..	..	..	..	..	8	36
$Cc^r\times Cc^r$	2	22	..	..	..	..	..	..	..	5	..	..	27
$Cc^d\times Cc^a$	1	10	..	..	..	..	..	..	3	..	..	..	13
$Cc^k\times Cc^k$	1	13	5	..	..	..	..	..	..	..	..	..	18
$CC\times C-$	3	34	..	..	..	..	..	..	..	..	..	..	34

TABLE 21

The differences in the grades of sepia of young of different genetic constitution born in the same litters in experiments J and K.

LITTER MATES	DIFFERENCE IN GRADE WITHIN LITTER												NUMBER	AVERAGE DIFFERENCE	AVERAGE DIFFERENCE FROM TABLE 11
	−3	−2	−1	0	1	2	3	4	5	6	7	8			
$c^k c^r - c^d c^a$	..	..	..	..	..	..	..	..	1	..	1	..	2	6.0	6.5
$c^r c^r - c^d c^a$	..	..	..	..	..	..	..	..	1	..	1	..	2	6.0	6.1
$c^k c^d - c^d c^a$	..	..	..	..	..	..	1	2	6	3	4	1	17	5.6	5.5
$c^d c^r - c^d c^a$	..	..	..	..	1	..	3	5	6	1	1	2	19	4.7	5.0
$c^k c^a - c^d c^a$	..	..	..	..	..	..	9	6	10	6	2	..	33	4.6	4.5
$c^d c^d - c^d c^a$	..	..	..	..	..	5	..	5	5	2	..	..	17	3.9	2.9
$c^r c^a - c^d c^a$	1	..	1	9	4	3	1	..	..	..	..	..	19	0.5	1.5
$c^k c^r - c^r c^a$	..	..	..	..	..	1	2	..	..	13	2	..	18	5.6	5.0
$c^r c^r - c^r c^a$	..	..	..	..	..	..	7	6	7	10	..	..	30	4.7	4.6
$c^k c^d - c^r c^a$	..	..	..	..	..	..	1	..	1	..	1	..	3	5.0	4.0
$c^d c^r - c^r c^a$	..	..	..	..	..	3	6	2	1	1	..	..	13	3.3	3.5
$c^k c^a - c^r c^a$	..	..	..	2	2	1	4	10	..	..	..	..	19	3.0	3.0
$c^r c^r - c^d c^d$	..	..	..	..	..	1	..	3	..	..	..	..	4	3.5	3.2
$c^d c^r - c^d c^d$	..	..	..	3	10	10	8	..	..	..	..	..	31	1.7	2.1
$c^r c^r - c^d c^r$	..	..	..	4	3	7	..	..	..	..	..	..	14	1.2	1.1
$c^k c^k - c^k c^a$	..	..	..	1	1	11	..	..	..	..	..	..	13	1.8	1.6
$c^k c^r - c^k c^a$	..	..	..	..	1	11	3	..	..	..	..	..	15	2.1	1.9
$c^k c^d - c^k c^a$	..	..	..	..	9	3	..	..	..	..	..	..	12	1.2	0.9

THE INHERITANCE OF SEX-LIMITED BILATERAL ASYMMETRY IN BRUCHUS[1]

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THE ORIGIN OF THE CHARACTER

The wild-type female, described in detail in previous publications, (BREITENBECHER 1921, 1922, 1923) has two black spots bilaterally located on each elytrum, while the wild male has no spots but transmits the genes (*ss*) for black spots. On October 23, 1922, there appeared in my cultures of *Bruchus quadrimaculatus* Fabr. an abnormal female with two red spots on her right elytrum instead of black spots, which are normally found on both elytra of the wild-type female. This unilateral insect originated from a homozygous culture (*RRss*) pure for red elytra and black spots. In cultures of this unilateral mutation, the abnormality, red spots on the right elytrum, and black spots on the left, did not breed true for this asymmetrical trait, but many females were found with the left elytrum

[1] The major portion of this experiment was conducted at the UNIVERSITY OF OKLAHOMA. It was completed at Woods Hole, Massachusetts, where the superior advantages of the MARINE BIOLOGICAL LABORATORY were enjoyed through the kindness of Doctor FRANK R. LILLIE.

black spotted and the right elytrum red spotted, while many manifested the original type of spotting. The males, however, in the homozygous mutant cultures, for either type of female, were always non-spotted. The size of the spots varied from four minute patches to quite large ones. For these reasons, "piebald" seemed the most appropriate name for this mutation.

MATERIALS AND METHODS

The problem here is concerned only with elytra color and its spotting; hence, for each of the types described, only such traits will be discussed. The wild-type females had tan elytra with black spots, as previously shown (BREITENBECHER 1921, 1923). The piebald females were crossed with males of another (*RRSS*) type in order that the unilateral piebald black spot might be more distinctly visible on a red background. Two types of piebald females were discovered: One (RB) had red spots only on her left elytrum with black spots on her right elytrum; while the other (BR) had black spots on the left elytrum with red spots on the right elytrum. All piebald males, for both kinds of females, appeared alike, having somatically tan non-spotted elytra. Single pair matings were used throughout this test. Virgin females were obtained by removing them with a knife from the cowpeas a few hours before they emerged. The cowpeas were sterilized in Mason jars kept at a temperature of 50°C for one hour. Each pair was placed in a two-ounce bottle, filled with these cowpeas, and plugged with cotton. Humidity was provided by placing several cultures in glass battery jars filled with a layer of water. Each container was covered with a glass plate and sealed with vaseline. Each jar with its insects was kept in a constant-temperature oven at 40°C. A generation would appear in about three weeks.

FORMULAE

The formulae used take into account both the sex-limited traits involved as well as both types of piebald females. The genes, *pp*, stand for the homozygous piebald recessive mutation.

The two types used are as follows:

(1) The normal type
  (a) Females. Two bilateral red spots on each elytrum (*PP*).
  (b) Males. Non-spotted with tan elytra (*PP*).

(2) The piebald type
  (a) Females. Elytra spotting of two kinds (*pp*).
    RB elytra: left, red spots; right, black spots.
    BR elytra: left, black spots; right, red spots.
  (b) Males. All with non-spotted elytra (*pp*).

THE EXPERIMENTAL RESULTS

In the tests that follow, each individual carried some combination of the following factors: *PP*, *Pp*, *pP* and *pp*. The piebald cultures were crossed with stocks having *RR* genes, homozygous for red elytra, and *SS* factors, pure for red spots on the elytra, in order to contrast the black

TABLE 1

P_1: A piebald female having red spots on her right elytrum and black spots on her left elytrum × a non-spotted male homozygous for red elytra color and red-spotted elytra.

F_1: No piebald females, 23 females with normal bilateral red-spotted elytra, and 25 non-spotted males.

PAIR NUMBER	F_2 ELYTRAL SPOTTING				
	Females			Males No spots	Ratio Red-spotted : piebald
	Red spots	Piebald			
		R B*	B R†		
60.1	29	0	2	26	14.5:1
60.2	37	3	1	33	9.2:1
60.3	40	4	2	74	6.7:1
60.4	0	0	0	25	0.0:0
60.5	20	2	3	31	4.0:1
60.6	34	1	5	44	5.7:1
60.7	18	2	1	30	6.0:1
60.8	16	2	2	25	4.0:1
60.9	18	2	3	24	3.6:1
60.10	46	5	4	40	5.1:1
60.11	37	5	2	36	5.3:1
60.12	51	1	3	37	12.7:1
60.13	19	2	1	21	6.3:1
60 14	14	0	0	17	14.0:0
60.15	6	1	2	8	2.0:1
60.16	29	1	3	30	7.2:1
60.17	19	2	0	21	9.5:1
60.18	9	1	2	11	3.0:1
Totals 18 pairs:	442	34	36	533	6.3:1

* R B indicates a female having red spots on the left elytrum and black spots on the right one.

† B R indicates a female having black spots on the left elytrum and red spots on the right one.

piebald spotting on either elytrum with the background of a pure-red elytrum. The piebald mutation, having black spots on either elytrum was represented by the genes *pp*, while the normal type, having bilateral red elytra spots, transmitted the factors, *PP*, *Pp* and *pP*. As a result of such a cross, the actual genetic formulae for all of these traits were *RRSSPP*, *RRSSPp*, *RRSSpP* and *RRSSpp*. Since every individual was homozygous for the *RRSS* genes, these unnecessary combinations have been omitted from all tables and from the discussion which follows.

The inheritance of the first piebald female

The complete data for two generations of the descendants of the first piebald female crossed with a normal non-spotted male, are given in table 1. The piebald mother had two red spots on her right elytrum and

TABLE 2

P_1: Piebald BR female (pp)×non-spotted male (PP) pure for red spots.
F_1: Red-spotted females(Pp) and non-spotted males (Pp).

PAIR NUMBER	F_1 ELYTRAL SPOTTING	
	Red-spotted females	Non-spotted males
307	9	12
304	14	4
300	6	2
293	1	10
282.6	6	2
282.5	15	15
282.4	13	13
282.3	3	3
282.1	7	7
274	5	11
272	8	12
271	10	14
269	11	8
267	18	15
266	20	11
265	11	19
264	21	15
263	8	6
262	16	19
260	15	8
259	18	9
258	13	15
245	20	21
242	16	22
231	16	0
229	26	17
224	13	13
218	20	33
217	18	29
215	20	23
Totals.....	397	408
Expected.....	*402.5*	*402.5*

two black ones on her left elytrum. She was bred to a normal, tan-elytra, non-spotted male homozygous for red spots and tan elytra. Their F_1 offspring consisted of 23 females with normal, bilateral red-spotted elytra,

no piebald females, and 25 non-spotted males. This test indicated that piebald was a recessive. Eighteen of these F_1 pairs were mated singly. The progeny of the above-mentioned pairs totaled 442 bilateral red-

TABLE 3

The same tests as enumerated in table 2.
P_1: Piebald, BR female (pp)×non-spotted male (PP) pure for red spots.
F_1: Red-spotted females (Pp) and non-spotted males (Pp).

PAIR NUMBER	F_2 ELYTRAL SPOTTING	
	Red-spotted females	Non-spotted males
196	23	8
193	26	14
192	24	7
189	3	0
187	13	15
184	31	32
180	16	9
172	3	4
170	9	23
165	14	0
156	8	10
155	10	12
131	1	4
128	12	13
126	7	4
125	12	12
121	16	17
113	11	8
112	12	25
99	15	19
95	3	5
94	15	28
92.3	30	37
92.2	14	27
92.1	13	13
89	17	25
83	13	21
76	7	12
75	10	16
73	17	19
70	36	32
Totals.....	441	471
Expected.....	*456*	*456*

spotted females, 70 piebald females (34 were of the RB type and 36 of the BR kind), and 533 non-spotted males. This gives an actual ratio of 6:1, when the expected ratio should be 3:1 in the F_2 generation. The discrep-

ancy is due to the fact that the piebald character is in many instances very minute. Therefore, during the earlier stages of the experiment, the spots frequently escaped observation and for that reason were not recorded. Hence, the data from table 1 is not added to those of the remaining tables.

Piebald BR females (pp) mated with normal males (PP)

Accurate breeding tests in which homozygous piebald (*pp*) females were crossed with normal homozygous (*PP*) males, were also conducted. The parents in thirty separate instances were piebald BR females (*pp*), which were bred to non-spotted, normal males (*PP*). The F_1 offspring were normal, bilateral red-spotted females (*Pp*) and normal, non-spotted males, in approximately 1:1 sex-limited ratio, thus indicating that the piebald character is recessive. This set of tests is recorded in table 2.

Table 3 is a continuation of the same test given in table 2. In this experiment like-parents, piebald BR females (*pp*), were mated with normal, non-spotted males (*PP*). The data included tests for 31 separate P_1 pairs. Their F_1 progeny consisted of 441 bilateral red-spotted, heterozygous females (*Pp*), and 471 non-spotted, heterozygous males (*Pp*). The same sex-limited, 1:1, ratio is therefore evident. Hence, the conclusions from the data given in tables 2 and 3 prove that when a piebald BR female is bred to a normal non-spotted male (*PP*), all offspring are heterozygous (*Pp*) with piebald as a recessive.

Piebald RB females (pp) bred to normal males (PP)

The information relative to such crosses is given in table 4. The P_1 parents consisted of a piebald RB female (*pp*) mated with a normal non-spotted male (*PP*). The F_1 progeny was heterozygous (*Pp*) and appeared normal. The female offspring from these parents appeared red-spotted, while the males were non-spotted. Forty separate P_1 pairs gave 558 heterozygous normal red-spotted (*Pp*) females and 629 heterozygous normal non-spotted (*Pp*) males. Again a 1:1 sex-limited ratio is manifest. Therefore, the data from tables 2, 3 and 4 prove that when any piebald (*pp*) female, whether a BR or an RB one, enters the cross with a normal non-spotted (*PP*) male, the F_1 offspring is always normal and no piebald appears, thus indicating that the trait is recessive.

The inheritance of a Pp female and a Pp male

The offspring from heterozygous, *Pp*, individuals is tabulated in table 5. Each F_1 pair consisted of a red-spotted normal (*Pp*) female and a normal non-spotted (*Pp*) male. The thirty-two separate F_1 pairs totaled in the

TABLE 4

P_1: Piebald, RB female ($p\mathfrak{p}$)×non-spotted male (PP) pure for red spots.
F_1: Red-spotted females ($P\mathfrak{p}$) and non-spotted males ($P\mathfrak{p}$).

PAIR NUMBER	F_1 ELYTRAL SPOTTING	
	Red-spotted females	Non-spotted males
306	1	0
296	3	3
294	8	19
281	9	5
268	13	10
257	22	11
248	13	13
239	9	12
237	21	15
232	16	16
214	9	7
211	28	24
200	24	19
199	25	38
198	6	7
197	19	28
183	24	8
181	3	5
179	5	19
177	18	18
176	20	15
175	27	15
174	11	11
168	14	10
163	12	0
157	17	15
127	8	9
123	12	12
120	10	10
119	9	11
107	16	29
103	21	29
97	18	35
96	11	18
91	23	20
90	10	12
84	21	19
80	26	41
71	7	13
67	10	16
Totals.....	588	629
Expected.....	*608.5*	*608.5*

TABLE 5

F_1: Red-spotted female (Pp)×non-spotted male (Pp).

F_1 PAIR NUMBER	F_2 ELYTRAL SPOTTING			
	Females			Males
	Red-spotted (PP, Pp, pP)	Piebald (pp)		Non-spotted (PP, Pp, pP, pp)
		RB	BR	
309	13	2	3	19
299	12	2	2	21
297	15	6	0	23
295	21	4	3	25
292	11	2	2	12
291	9	1	2	16
290	5	1	1	15
289	12	2	2	26
284	2	0	1	3
281.3	13	0	4	22
281.2	17	3	4	20
281.1	12	3	2	20
261	12	2	2	10
243	27	3	6	23
240	20	7	2	34
234	3	1	0	2
227	17	4	4	23
205	10	1	2	21
195	20	4	1	14
162	19	0	8	18
159	7	1	2	11
154	15	2	2	15
153	2	1	0	13
133	16	3	2	17
130	18	3	3	24
124	21	3	2	21
117	5	1	2	5
110	11	2	1	22
104	8	2	0	10
87	13	3	0	23
86.1	4	2	0	9
86	14	4	2	10
85	17	2	3	17
84.1	23	3	4	32
82	11	2	1	17
81.2	24	3	2	26
81.1	21	7	2	24
81	20	5	1	19
80.1	21	4	2	29
79.3	13	0	4	23
79.1	16	4	0	16
79	11	4	0	21

TABLE 5 (continued)

F_1 PAIR NUMBER	F_2 ELYTRAL SPOTTING			
	Females			Males
	Red spotted (PP, $P\phi$, ϕP)	Piebald ($\phi\phi$)		Non-spotted (PP, $P\phi$, ϕP, $\phi\phi$)
		RB	BR	
77	25	5	2	16
75.3	14	3	2	21
75.2	12	2	3	17
74	16	3	2	21
73.7	18	2	3	18
72	3	1	0	5
69	31	2	7	38
68.2	6	2	1	9
68	22	5	2	38
65.1	30	6	2	46
62.9	19	3	3	33
62.7	40	7	4	51
62.5	24	3	4	24
62.4	18	3	3	25
62.2	18	3	1	22
62.1	13	4	1	25
Totals.....	897	163	127	1192
Piebalds.....	897	290		1192
Expected, 3:1:4	*900*	*300*		*1200*

F_2 generation, 411 red-spotted (PP, $P\phi$, ϕP) females, 143 piebald ($\phi\phi$) females (75 were of the RB type and 68 of the BR kind), and 547 non-spotted (PP, $P\phi$, ϕP, $\phi\phi$) males. In table 6, which is a continuation of table 5, twenty-six separate F_1 heterozygous pairs ($P\phi$) produced in the F_2 generation, 486 red-spotted (PP, $P\phi$, ϕP) females, 147 piebald ($\phi\phi$) females (88 were of the RB kind and 59 of the BR type), and 645 non-spotted (PP, $P\phi$, ϕP, $\phi\phi$) males. The totals from table 5 are 897 red-spotted females, 290 piebald females, of which 163 were RB and 127 BR, and 1192 non-spotted males. This result approximates a 3:1:4 sex-limited ratio, or actually a 3:1 ratio, since all the males appeared alike. There were also a few more RB than BR piebald females enumerated in this experiment.

Backcross test: A PP female × a Pφ male

Homozygous normal bilateral red-spotted (PP) females were mated to non-spotted heterozygous ($P\phi$) males. From 16 P_1 separate pairs, a total progeny of 291 normal red-spotted (PP, $P\phi$) females, and 286 normal,

non-spotted (*PP*, *Pp*) males was produced, which is a 1:1 sex-limited ratio. This shows the complete dominance of the normal character over the piebald. The data are given in table 6.

TABLE 6

Backcross test.
P_1: 1 Red-spotted female (PP)×1 non-spotted male (Pp).

P_1 PAIR NUMBER	F_1 ELYTRAL SPOTTING	
	Red-spotted females (*PP*, *Pp*)	Non-spotted males (*PP*, *Pp*)
288	7	13
286	11	15
285	25	16
84.2	12	16
80.2	16	23
77.8	30	30
77.1	14	16
75.1	39	21
73.4	18	26
73.3	16	17
73.2	6	0
71.3	12	10
71.2	14	16
71.1	28	30
70.2	28	25
70.1	15	12
Totals	291	286
Expected	*288.5*	*288.5*

Backcross test: A Pp female×a PP male

This test, the complete data of which are given in table 7, was the reciprocal of the previous one. The P_1 parents were heterozygous red-spotted (*Pp*) females and homozygous non-spotted (*PP*) males. Nineteen separate pairs mated produced 325 normal red-spotted (*PP*, *Pp*) females and 307 normal non-spotted (*PP*, *Pp*) males, which is a 1:1 sex-limited ratio. The results further confirm the previous tests, which showed that the normal trait is dominant to the recessive piebald.

Backcross test: A BR piebald (pp) female×a Pp male

Homozygous (*pp*) BR piebald females bred to heterozygous non-spotted (*Pp*) males gave from the 12 separate pairs mated in the F_1 generation, a total of 100 normal red-spotted (*Pp*) females, 37 RB piebald (*pp*) females, 51 BR piebald (*pp*) females, and 209 non-spotted (*Pp*, *pp*) males. By adding the two types of piebald females, 88 piebald (*pp*)

females are obtained. The observed ratio is 100:88:209 which approximates a 1:1:2 sex-limited ratio. This experiment proves that the characters, normal and piebald, segregate as a 1:1 ratio, if only the two types of piebald females are added. It illustrates that the pied trait is a recessive to the normal. However, the RB piebald females in this test did not breed true for the RB type but again produced two kinds, the RB and BR, in about equal numbers. No male manifested the piebald character. The results are given in table 8.

TABLE 7

Reciprocal backcross test.
P_1: 1 red-spotted (Pp) female×1 non-spotted (PP) male.

P_1 PAIR NUMBER	F_1 ELYTRAL SPOTTING	
	Females Red-spotted (PP, Pp)	Males Non-spotted (PP, Pp)
69.1	7	5
62.6	1	2
62.3	33	30
61.1	20	15
61.4	0	2
61.5	27	21
61.6	18	22
61.9	22	29
61.10	15	22
61.11	0	3
61.12	8	7
61.13	5	12
61.14	3	9
61.15	12	4
61.16	13	2
61.52	26	17
61.51	24	20
61.42	22	24
61.43	69	61
Totals.....	325	307
Expected.....	*316*	*316*

Backcross test: An RB piebald (pp) female×a Pp male

This test is the same as the previous one with the exception that an RB piebald female was used instead of a BR female. The experiment is given in table 9. The parents were homozygous RB (pp) females and heterozygous, non-spotted (Pp) males. Twenty separate pairs produced 176 normal red-spotted (Pp) females, 105 RB piebald (pp) females, 59 BR piebald (pp) females, and 356 non-spotted (Pp, pp) males. By adding

together the two kinds of piebald (*pp*) females, 164 were obtained. The actual ratio was 176:164:356, approximating a 1:1:2 sex-limited ratio. This test proves that piebald is a recessive homozygous trait when the two types, dextral and sinistral, are added. Lastly, the two different piebald patterns, RB and BR, did not breed true for each different kind, but each produced both types in about equal numbers.

TABLE 8

Backcross test.
P_1: A piebald BR female (pp)×a non-spotted male (Pp).

F_1 PAIR NUMBER	F_1 ELYTRAL SPOTTING			
	Females			Males Non-spotted (*Pp*, *pp*)
	Red-spotted (*Pp*)	Piebald (*pp*)		
		RB	BR	
282.2	2	0	2	3
247	8	7	0	16
246	9	0	5	15
244	3	0	3	13
216	17	0	11	27
210	16	0	15	22
186	8	11	0	19
79.2	15	4	7	15
78	2	1	2	9
79.9	6	7	1	34
77.2	5	4	0	13
66.1	9	3	5	23
Totals.....		37	51	
	100	88		209
Expected, 1:1:2	*99*	*99*		*198*

A pp female×a pp male

The result of this test is given in table 10. Each pair mated consisted of a piebald (*pp*) RB female and a non-spotted (*pp*) male, both of which were homozygous for the piebald factor. Twelve separate pairs gave a total of 109 RB piebald (*pp*) females, 100 BR piebald (*pp*) females and 213 non-spotted (*pp*) males. By adding the two types of piebald (*pp*) females, a total of 209 piebald females is obtained, which approximates a 1:1 sex-limited ratio. The ratio is a sex-limited one because the piebald trait is not visible in the male. It further demonstrates that this mutation bred pure for piebald, when the two types of piebald females were added together. Furthermore, the RB piebald females were about equal, though

the BR pattern was slightly in excess. Lastly, this experiment proved that the homozygous RB piebald female mated with a non-spotted male, homozygous for piebald, did not breed true for the RB unilateral pattern, but always produced two types, the RB and BR, in about equal numbers.

TABLE 9

Backcross test.

P_1: A piebald RB female (pp)×a non-spotted male (Pp).

F_1 PAIR NUMBER	F_1 ELYTRAL SPOTTING			
	Females			Males Non-spotted (Pp, pp)
	Red-spotted (Pp)	Piebald (pp)		
		RB	BR	
235	3	4	0	8
228	9	5	5	27
226	5	3	9	2
225	19	8	2	26
223	4	5	0	13
282	8	0	6	16
208	12	10	3	27
205	9	7	4	24
204	13	10	0	14
202	24	16	5	36
201	11	10	2	22
188	6	6	0	25
185	1	1	0	7
173	5	3	1	7
169	5	4	0	15
160	12	2	10	23
118	4	0	3	5
777	6	0	9	14
773	11	5	4	18
*628	9	6	2	27
Totals.....		105	59	
	176	164		356
Expected, 1:1:2	*174*	*174*		*348*

A summary of the RB and BR piebald females

A summary of the two kinds of piebald females, the RB and the BR types, is given in table 11. These totals show that for the piebald females, 448 manifested the RB spotting and 373 the BR pattern; that is, those females having the red spots on the left elytrum and black ones on the right were more frequent than those having black spots on the left elytrum

and red spots on the right. The numbers for all tests were about equal.

The conclusions from this set of tests are, first, that piebald is a sex-limited recessive, visible only in the females, and second, that the character is always seen on either the left or right elytrum, never on both at the same time.

TABLE 10

P_1: A piebald R B female ($\varphi\varphi$) × a non-spotted male ($\sigma\sigma$).

F_1 PAIR NUMBER	F_1 ELYTRAL SPOTTING		
	Females Piebald ($\varphi\varphi$)		Males Non-spotted ($\sigma\sigma$)
	R B	B R	
304	0	1	3
222	15	15	18
221	1	0	12
213	5	14	14
212	24	0	25
209	12	5	24
190	7	11	19
182	2	0	2
129	11	6	23
116	9	17	29
111	12	13	20
109	11	18	24
Totals	109	100	
	209		213
Expected	*211*		*211*

TABLE 11

A summary of the piebald females ($\varphi\varphi$).

TOTALS FROM TABLE NUMBER	PIEBALD FEMALES	
	RB	BR
1	34	36
5	75	68
6	88	59
9	37	51
10	105	59
11	109	100
Totals	448	373

DISCUSSION

Since the two bilateral pigmented areas of Bruchus have definite boundaries, appearing always in the same position on the elytra of the females, they form a pattern resembling, somewhat, the many piebald traits in animals. Aside from the sex-differences, they suggest ALLEN'S "centers of pigmentation" (ALLEN 1904), especially since there are other pigmented areas located elsewhere on this weevil, which are not sex-limited. Careful examination of the several available species of Bruchidae show that the sexes are not easily distinguished, except in *B. quadrimaculatus*, though each species manifests a design peculiar to its kind.

In Bruchus, symmetry is externally visible in the duplication of spots, patterns, colors, elytra, antennae, legs, etc., while asymmetry is rarely manifested externally. Inherited asymmetry is illustrated by this piebald mutation, originating from purely symmetrical insects.

In order to study the inheritance of this trait successfully, it was necessary to contrast the normal bilaterality with the abnormal asymmetry. This was accomplished by injuring the pupae on one side, thus producing asymmetrical elytra colors in the adult female. Such abnormalities were not inherited, though some were similar to the elytral spot-color mosaics, a list of which has been published (BREITENBECHER 1922). These were also non-inherited, but were interpreted, at that time, as somatic mutations. The most frequent mosaic type, red spots on one elytrum and black spots on the other, resembles this piebald mutation, except for its heritability.

The actual cause of sex-limited differences in insects has not been conclusively demonstrated. One of the theories advanced by GOLDSCHMIDT and FISCHER (1922) in explanation of sex-controlled characters in Lepidoptera seems to apply to these traits in Bruchus, since the male shows himself a fraction of a day earlier than the female. However, only twenty percent of the mutations in this weevil are sex-limited, although in every mutation discovered the males issued at the same time, whether sex-limited or not; hence, some other explanation should account for the remaining eighty percent, unless it is assumed that such characters develop more rapidly. According to BROOKS (1922) the Y chromosome is absent in Bruchus; therefore, BRIDGES'S (1922) interpretation that both sexual and sex-limited characters depend upon "modifiers" within the X chromosome of Drosophila, upon further investigation, may be found to be equally applicable to Bruchus.

The results of selection are negative. Since the males for both types of pied females appear alike, it is impossible to distinguish them. It is not

unreasonable to suppose that in this experiment, comprising a great number of matings, an RB female will have been mated with an RB male at least half the time, and that their offspring should breed true for this type; but such pairs always produced, on the average one dextral female, one sinistral female and two normal males, regardless of the character of the parents which entered the test.

The piebald trait for Bruchus is an instance of bilateral asymmetry. The bilaterality is shown by the arrangement of the two spots on each elytrum. The asymmetry is manifested by the color differences of these spots. If this pied character is considered as unilateral, the black spots representing this condition, then the red spots might be the result of normal genes. Or, if the bilateral red spots should be the trait, then a unilateral inhibitor might make the color difference. There seems to be some delicate adjusting mechanism which shifts the asymmetrical spotting right and left according to chance, since equal numbers of dextrals and sinistrals is produced.

CONCLUSIONS

1. The sexes in homozygous piebald cultures are dissimilar in appearance. The female has two black spots on one elytrum and two red spots on the other, or *vice versa*, equal numbers dextral and sinistral. The male has no elytra spots and is without dextral or sinistral differences.

2. This trait is sex-limited although it is transmitted equally by both sexes.

3. The piebald mutation is a recessive, the typical recessive frequency being obtained by adding together the dextral and sinistral females.

4. This character is called piebald, since it varies in the amount of spotting and size of spots.

5. Symmetry is normally manifested in this insect by the duplications of spots, patterns, colors, antennae, elytra, legs, etc., while asymmetry is rarely seen externally.

6. This piebald-asymmetry is inherited, while asymmetries discovered for mosaics and from experimental injuries were not.

7. This trait has a normal bilaterality and symmetry in the pupal state, its asymmetry not being visible until the insect becomes adult.

8. Unilateral characters in animals are usually limited to one body side. However, this type of unilaterality is not found in this piebald trait, since dextral females always produce both dextral and sinistral insects in equal numbers.

9. Probably some delicately adjusting mechanism shifts this asymmetry right or left according to chance.

10. Lastly, the piebald trait for Bruchus is an instance of inherited bilateral asymmetry.

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INTERSPECIFIC HYBRIDIZATION IN NICOTIANA. II. A TETRAPLOID *GLUTINOSA-TABACUM* HYBRID, AN EXPERIMENTAL VERIFICATION OF WINGE'S HYPOTHESIS

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Numerous investigations have shown that in plants the chromosome numbers of the species of a genus are often in arithmetical progression. Excellent examples are afforded by Triticum, $n=7$, 14 and 21; by Rosa, $n=7$, 14, 21, 28; and by Chrysanthemum, $n=9$, 18, 27, 36 and 45. Appeal has often been made to tetraploidy as a method of increase in chromosome number, but WINGE (1917) has pointed out that successive doubling of chromosome number would give rise to geometrical rather than arithmetical series, and has suggested as an alternative hypothesis interspecific hybridization followed by doubling of chromosome number. The process suggested by WINGE would establish tetraploid interspecific hybrids having 2 (n_1+n_2) chromosomes, where n_1 and n_2 represent the haploid numbers of the parent species; and since such forms are essentially homozygous diploids, they may reasonably be expected to be fertile and constant. WINGE was unable, however, to present any experimental evidence in support of his hypothesis. In this article a preliminary account is given of a tetraploid hybrid of *Nicotiana glutinosa* and *N. tabacum*, and attention is invited to *Primula kewensis*, apparently a tetraploid *P. floribunda-verticillata* hybrid, which together offer the necessary experimental verification of the hypothesis.

The two species of Nicotiana employed in the present investigations are very distinctly different. *N. glutinosa* is particularly characterized by its villose pubescence; its distinctly petioled, cordate leaves; its bilabiate flowers; and its sparsely branched, racemous inflorescence. It is one of the most distinct species of the genus. *N. tabacum* is familiar to almost everyone as the tobacco of commerce. Descriptions and more complete illustrations of the forms employed in the experiments described below may be found in SETCHELL'S (1912) account of the genus. The chromosome number of *N. glutinosa* is $n=12$ (GOODSPEED 1923), of *N. tabacum*, $n=24$ (WHITE 1913, GOODSPEED 1923).

The two species have frequently been crossed. Reciprocal hybrids may be obtained, although hybridization is attended with some difficulty. Usually only a few viable seeds are produced in a capsule; in our experience an average of about ten or twelve. The F_1 hybrids are weak in germination and development, but they grow on to maturity. This, in brief, is the behavior which has been noted for all varieties of *N. tabacum* which have been tested, except one, the variety "Cuba" (cf. GOODSPEED 1915). From "Cuba" ♀ × *glutinosa* ♂ full capsules of seed are obtained. These seeds are of the same order of viability as pure seed of the species; the seedlings are vigorous; the hybrid plants develop to a height approximately equal to that of "Cuba"; and they branch profusely. GÄRTNER (1849) apparently also observed marked differences in the vigor of F_1 *glutinosa-tabacum* hybrids, when different *tabacum* varieties were employed; but as FOCKE (1881) points out, it is difficult to know how to judge these results because of the numerous discrepancies in GÄRTNER'S account of his observations. Despite these differences in vigor, the F_1 hybrids are always intermediate in appearance and they are apparently completely sterile. Numerous attempts to secure seed by backcrossing to the parental species under a variety of conditions have failed, and no seed has been found in open-pollinated capsules.

In 1922 from a single capsule of *glutinosa* ♀ × *tabacum* var. *purpurea* ♂, three plants were secured, which were grown under the garden number, 22062. Two of these plants were obvious hybrids. They were both small plants, about two feet in height, with few, slender branches and small leaves. The flowers exhibited a strong tendency towards the bilabiate shape of *N. glutinosa*, but the color was carmine, like that of *purpurea*. The leaves showed distinct evidences of *glutinosa* in their cordate shape. One of these plants was partially fertile, the other completely sterile. No other differences were noticed at that time. The third plant was very strikingly different from the other two; in fact, if our notes and memory may be depended upon, it was identical with the *purpurea* haploid which was obtained later (cf. CLAUSEN and MANN 1923). Unfortunately, we lost it during the winter of 1922-1923 because of unfavorable greenhouse conditions.

A number of flowers on the single partially fertile plant were hand-pollinated and gave selfed seed without difficulty. The capsules were harvested separately. In the season of 1923, 155 plants were obtained from one of these capsules. These, however, were set out in the field late in the season, and they did not mature. In 1924 a culture of 65 plants was grown under the garden number, 24123. For purposes of comparison

there was available at the same time a culture, 24192, of 15 F_1 plants of *purpurea* ♀ × *glutinosa* ♂. Much to our surprise, with one exception, the 65 F_2 plants of 24123 were uniform and almost identical with the F_1 plants of 24192. There were, however, important minor differences, which were found constantly to characterize the two populations. The F_1 plants were completely sterile. They set no seed on open-pollination, and twenty-five attempts at back-pollination with each of the parental species failed to give seed. Under these circumstances, capsules were retained for as long as three weeks, but in no case did they reach maturity. The plants of the F_2 population were reasonably fertile, and uniform in this respect. Large plump capsules were obtained from open-pollinated and hand-pollinated flowers and also from crosses with the parent species. These capsules contained a fair quantity of seed, but not so much as capsules of normal species.

The plants of the two populations exhibited a close correspondence in morphological characters. Both populations were very uniform. The F_2 plants had slightly, but constantly, larger flowers than F_1 plants, and the anthers were conspicuously larger. F_2 plants produced abundant pollen, most of the grains of which were normal in appearance: F_1 plants produced scanty pollen, consisting entirely of shrivelled empty grains. F_1 plants averaged about two feet in height, F_2 plants about a foot and a half. Despite the difference in height, which was probably due to their unfavorable start in the flats, the general impression given by F_2 plants was that of a slight enlargement to scale of characters of F_1, aside from those features obviously connected with the difference in fertility.

One F_2 plant stood out from the rest by reason of its remarkable robustness. This plant eventually attained a height of six feet, and produced numerous stout branches. Despite the difference in size, however, the general morphological characters were those of the other plants of the population on an enlarged scale. Vegetative characters were proportionately enlarged, flower size only slightly. The plants of this population were all very weak as seedlings, and they grew very feebly during the time they were in flats. It is believed that the general small size of the plants in the population was due to this stunting during their early growth and that 24123P55, the robust individual, merely by some fortunate chance overcame this difficulty.

The uniformity of F_2 and its close resemblance to F_1 immediately suggested the need for cytological examination. Excellent aceto-carmine smears of pollen mother cells were easily secured; the stage of development of anthers containing them in proper condition being rather later

than is usually the case. Examinations were made of material from several plants, including the robust plant described above, which gave exactly the same results as the others. The general impression of the cytological figures was one of regularity of meiotic division rather different from the irregular distribution seen in normal F_1 *glutinosa-tabacum* hybrids. Numerous counts of first-metaphase figures showed 36 bivalents. In a few instances it was possible to count both metaphase plates in the second division, and to determine that each contained 36 chromosomes. There was of course some doubt as to the exact count in a number of figures, but only to the extent of one or two chromosomes. There were minor irregularities in distribution, evidenced by precocious splitting, lagging, and microcyte formation; but these features, while noticed, were not studied in detail. There is no doubt that the chromosome number of the plants of this population was uniformly $n = 36$, $2n = 72$.

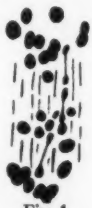

Fig. 1

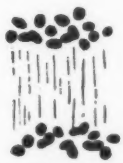

Fig. 2

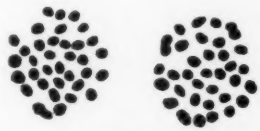

Fig. 3

FIGURE 1.—Portion of an anaphase of the normal F_1 *glutinosa-tabacum* hybrid.
FIGURE 2.—The same of the tetraploid hybrid.
FIGURE 3.—Homotypic metaphase, polar view, of the tetraploid hybrid.

Pollen-mother-cell heterotypic anaphase conditions in the sterile F_1 *glutinosa-tabacum* hybrid and in the tetraploid hybrid are illustrated in figures 1 and 2, while figure 3 shows two homotypic metaphase plates of the tetraploid, each polar view containing 36 chromosomes. Figure 1 was drawn from fixed material, the other two figures from aceto-carmine preparations. As will be noted (figure 1), the behavior of the bivalent and univalent chromosomes closely parallels that found in the F_1 *tabacum-sylvestris* hybrid elsewhere described (GOODSPEED 1923). The bivalent partners are approaching the poles while the univalents are in the equatorial zone, either dividing or preparing to divide. In the tetraploid, on the other hand, there appear to be no univalent chromosomes and the bivalent partners move in regular fashion to the poles. No attempt is made in either figure 1 or 2 to represent the full chromosome complement.

Pollen conditions are illustrated in figures 4 and 6 for the tetraploid hybrid and in figure 5 for the normal sterile F_1. These figures are repro-

duced from photomicrographs of pollen preparations stained with aceto-carmine. As will be noted, the pollen of the normal hybrid consists exclusively of shrivelled grains devoid of contents. The pollen of the tetraploid hybrid consists mostly of large grains apparently normal in protoplasmic contents. Measurements were made of pollen grains of the tetraploid hybrid and of its *tabacum* parent, but unfortunately no pollen of *glutinosa* was available at the time measurements were made. The average diameter of pollen grains in the tetraploid hybrid was found to be 46.3 microns, of *tabacum*, 36.7. The volumes are therefore, in the ratio of approximately 2 : 1 (106 : 49).

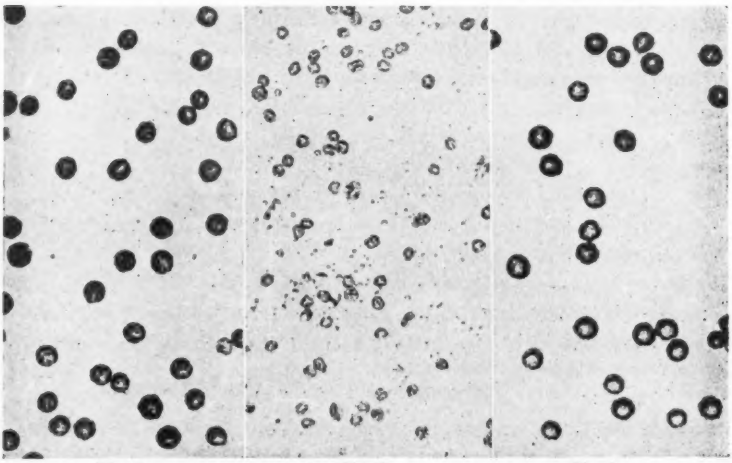

Fig. 4 Fig. 5 Fig. 6

FIGURE 4.—Portion of a photomicrograph of pollen of the tetraploid *glutinosa-tabacum* hybrid, 24123P55.

FIGURE 5.—Of the normal F_1, 24192P4.

FIGURE 6.—Of another plant of the tetraploid hybrid, 24123P58. The preparations were stained in aceto-carmine and the photomicrographs were taken at the same magnification.

The cytological findings supply an obvious explanation for the uniformity and constancy of this hybrid. Since in *glutinosa*, $n = 12$, and in *tabacum*, $n = 24$, the F_1 hybrid normally has 36 chromosomes. This was undoubtedly the case in the sterile F_1 described above. The original fertile F_1 plant, 22066P2, must have arisen from a doubling of the chromosome number immediately or soon after fertilization, by which a tetraploid hybrid with 36 pairs of chromosomes was produced. Such a plant may be represented by the chromosomal formula, 12 GG+24 TT;

and, if *glutinosa* and *tabacum* homologues pair regularly, fertility and constancy follow as a matter of course, for every gamete would then contain 12 *glutinosa* and 24 *tabacum* chromosomes. If this explanation is correct, an interspecific hybrid may be expected to become fertile and constant by simple doubling of its chromosome number.

These observations naturally recall the case of *Primula kewensis*, the much discussed hybrid of *P. floribunda* with *P. verticillata*. According to accounts of its origin as described by Miss DIGBY (1912) and by the Misses PELLEW and DURHAM (1916), the original hybrid was sterile; but it eventually produced a fertile bud-sport which gave rise immediately to the fertile, comparatively constant form now known as *P. kewensis*. Miss DIGBY found that the chromosome numbers of *P. floribunda* and *P. verticillata* were both $n=9$ and $2n=18$, that the sterile hybrid had 18 chromosomes and the fertile *P. kewensis*, 36. *P. kewensis*, therefore, is evidently a tetraploid hybrid; and as WINKLER (1920) and RENNER (1924) suggest, this fact probably accounts for its genetic behavior. If it contains 9 pairs each of chromosomes of *P. floribunda* and *P. verticillata*, and homologues of each species pair regularly, the situation is exactly the same as that described in the tetraploid Nicotiana. It seems more reasonable to adopt this explanation of its chromosome number, since it accounts so well for the genetic results thus far obtained with it, rather than that of transverse fission suggested by FARMER and DIGBY (1914) on the basis of chromosome measurements, which has been accepted by GATES (1924) in his recent discussion of polyploidy.

The confirmation of WINGE'S hypothesis afforded by the instances described above extends only to establishment of the tetraploid chromosome condition, and not to the method of origin described by him. The establishment of the condition is evidently a mutational event, analogous to that which occurs in the establishment of the tetraploid condition in pure species. The tetraploid hybrid condition may, however, arise in a variety of ways: (1) by doubling of chromosome number immediately subsequent to fertilization; (2) by bud-variation in an F_1 interspecific hybrid; (3) by crossing together tetraploid representatives of two different species; and (4) by irregular distribution of chromosomes in an interspecific hybrid in which the chromosomes do not pair in meiosis, as suggested by COLLINS and MANN (1923). It may be possible, therefore, that tetraploid hybrids have the significance in the origin of new chromosome numbers ascribed to them by WINGE.

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THE CORRELATION OF CHARACTERS IN HYBRIDS OF *TRITICUM DURUM* AND *TRITICUM VULGARE*

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INTRODUCTION

In crosses between *durum* and *vulgare* wheats, correlation of certain *durum* characters has been reported. FREEMAN (1917) found that the *durum* hardness of grain was associated with *durum* shape of head. HAYES, PARKER and KURTZWEIL (1920) reported a correlation between rust-resistance and other *durum* characters, the greatest difficulty being experienced in securing *vulgare*-like segregates with rust-resistance. From his work on the chromosomes of wheat, SAX (1922) concluded that the

durum characters should be correlated on the one hand, and the *vulgare* characters on the other. Later (SAX 1923) he showed that in the F_3 segregates an actual correlation existed between chromosome number and several characters.

Nevertheless, HAYES and his co-workers (1920) did succeed in securing a few *vulgare*-like segregates which were rust-resistant, a result which has also been obtained by the writer, though according to my observations neither their resistant *vulgare*-like lines nor mine are as resistant as the *durum* parent. Moreover, almost every individual feature characteristic of *durum* wheats is also found in some one or few *vulgare* varieties, and *vice versa*. Some of these varieties are considered by PERCIVAL (1921) to be the result of hybridization.

There is very great need in some regions of developing a *vulgare* wheat with certain *durum* qualities, notably drought-resistance and rust-resistance. *Vulgare* varieties are known which have some degree of resistance to stem rust, but so far none has been found which is resistant to all the biologic forms of stem rust which are found in Western Canada. On the other hand, certain *durum* and emmer varieties are very highly resistant to all the biologic forms which have been discovered here. It is essential, therefore, to determine whether there is such a correlation that this and other characters can not be transferred to *vulgare* types.

THE CHARACTERS CONCERNED AND THEIR INDIVIDUAL INHERITANCE

In the experiments reported in the following pages the *vulgare* parent was the variety Marquis and the *durum* parent was a highly rust-resistant line selected from Iumillo. Thirteen pairs of characters which are readily distinguishable in these parents were chosen for study. Some of these characters, e.g., head form and condition of keel, distinguish nearly all *durum* varieties from nearly all *vulgare* varieties; others, such as length of beards, cannot be considered diagnostic. It was thought that these two kinds of characters might show significantly different behaviors. The characters in question are as follows:

Compactness

When the length of the head in centimeters is divided by the number of spikelets, the range of variation in the *durum* parent is from 0.33 to 0.39, while in the *vulgare* parent it is from 0.43 to 0.54. A similar difference exists between all *durum* and *vulgare* varieties, except that the club wheats, which are generally classified with *T. vulgare*, show the *durum* compactness.

In F_2 the range of variation is from 0.26 to 0.55, with a considerable number intermediate.

Head form

By this term is meant the ratio of the width (1-ranked side) to thickness (2-ranked side). In Iumillo this ratio varies from 0.7 to 1.0 while in Marquis it varies from 1.2 to 1.5. This is a characteristic difference between *durum* and *vulgare*, the only exceptions being a few *vulgare* varieties in which the two dimensions are equal. In F_2 the range of variation extends beyond the extremes of both parents and some plants show variations in different heads, or even in the same head.

Diameter of stem

In 1923 this varied in Iumillo from 1.0 to 1.5 mm measured at a point 2 cm from the base of the head, and in Marquis from 1.75 to 2.25. In F_2 the range of variation again extended beyond the parental extremes, and some plants showed considerable variation in different stems.

Beard length

In Iumillo the beards measure from 10 to 12 cm, in Marquis up to 2 cm. n F_2 the parental and all intermediate conditions are found, but there is a distinct massing of individuals with the shorter beards. The long-bearded condition is characteristic of all but a few varieties of *durum*, but *vulgare* varieties may be long- or short-bearded or beardless.

The remaining characters do not lend themselves to measurement, but are quite distinct in the parent types.

Keel

In *durum* wheats the keel of the outer glume is generally very prominent and extends the full length of the glume; in *vulgare* it is usually less pronounced and extends only part of the length, though in some varieties it is large and extends from tip to base. In Marquis it is better developed than in most *vulgare* varieties. In F_2 intermediate conditions are common.

Middle tooth

The apical tooth of the outer glume is long, sharp and slightly curved in Iumillo, whereas it is short and blunt in Marquis. This distinction applies to most, but by no means all, *durum* and *vulgare* varieties. In F_2 the variation again extends beyond the parental extremes, those longer than the *durum* extreme being few but very conspicuous.

Lateral tooth

In Iumillo this is short and situated close to the middle tooth; in Marquis it is much further away and gives a shoulder-like appearance to this portion of the glume.

Glume shape

In Iumillo the glume is long and narrow, in Marquis short and wide. These differences are generally applicable to *durum* and *vulgare* varieties, though exceptions occur.

Keel hairs

Long and numerous in Iumillo; short and scattered or absent in Marquis. In F_2 the parental conditions and intermediate ones with respect to both length and number are found.

Collar

The collar-like structure at the base of the lowest spikelet extends completely round nearly all the stems in Iumillo and only part way round the stem in Marquis in nearly all cases. In F_1 and some F_2 plants, the collar extends part way round some stems and all the way round others. These are recorded as intermediate.

Cavity of stem

Durum varieties usually have solid stems though some varieties have hollow ones with thick walls; *vulgare* stems are usually hollow with thin walls, though some varieties have solid stems. Iumillo and Marquis are typically *durum* and *vulgare*, respectively. In F_2 very few plants have as thin walls as Marquis, though many have well developed cavities.

Seed hairs

In Marquis there is a thick brush of long hairs at the stigma end of the kernel as in *vulgare* wheats, generally; in Iumillo there are a few short scattered hairs.

Seed form

In *durum* varieties generally the seed is longer, narrower and more tapering than in *vulgare*. In Marquis the bluntness and plumpness is very pronounced.

Other characters

The use of certain other characters was considered but was rejected because it was thought that they might give a false idea of correlation.

For example, the form of the spikelet is very different in the two species, being much broader in *vulgare* than in *durum*, but this form of spikelet very largely determines the character called head form (width : thickness) since width of head depends on width of spikelets. Similarly, the distribution of beards is very different in the parental races, but beard-distribution is in all wheats closely correlated with beard-length. Only those characters were chosen for which there is no external or evident physiological reason for correlation, or which can be separated as shown by the breeding results.

Table 1 shows the results of classifying 57 F_2 plants according to each of the 13 characters. The *vulgare* condition of a character is designated V, the *durum* condition D, intermediate I, intermediate but nearer *vulgare* IV, intermediate but nearer *durum*, ID. In such characters as collar and diameter of stem, I plants were those which had some stems *durum*-like and others *vulgare*-like. In every possible case an F_3 family was grown, though owing to sterility, these families were often small and sometimes missing. The F_2 classification was checked by the F_3 results. In a few cases, particularly of intermediate characters, it was necessary to transfer an F_2 plant to a different class because of the F_3 results.

TABLE 1

CHARACTER	COMPACTNESS	HEAD FORM	KEEL	MIDDLE TOOTH	LATERAL TOOTH	GLUME SHAPE	KEEL HAIRS	COLLAR	BEARDS	CAVITY OF STEM	DIAMETER OF STEM	SEED HAIRS	SEED FORM
V	15	9	14	22	14	10	20	17	26	9	26	33	13
IV	..	..	..	..	..	..	..	..	10	7	..	..	..
I	15	17	14	16	9	19	19	17	9	18	6	12	15
ID	..	..	8	..	..	..	..	..	7	..	..	..	..
D	27	31	21	19	34	28	18	23	5	23	25	12	29

It is difficult to bring the results given in this table into line with Mendelian ratios. Other investigators have reported Mendelian results for some of these characters, but I am unable to reconcile their results with these. In regard to almost every character, the proportion of intermediate F_2 plants is too small for a monohybrid ratio. And any interpretation which is more complex encounters difficulties with the F_3 results. In

general the offspring of plants intermediate for any character included a high proportion of *vulgare* plants and *durum* plants, and relatively few intermediates. The *vulgare* plants gave only *vulgares* or some intermediates, and with some characters a few *durum* plants. The *durum* plants behaved similarly. The F_3 results are not given in detail for each character, since we are concerned primarily with the correlation of the whole group of characters.

THE CORRELATION OF CHARACTERS

Experimental data

In table 2 the condition of each of the 13 characters in each of the 57 F_2 plants is shown. The data are given in this extended form because it was desired to ascertain the degree of correlation amongst the whole 13 characters, not merely by pairs, and to compare different plants in regard to the amount of correlation. The letters have the same meaning as in table 1. In each case the classification was confirmed or corrected by reference to the F_3 plants. At the right of the table is shown the number of characters (out of the 13) in each category for each plant.

Analysis of data

In this table it will be observed that the plants fall into three groups: (1) those with *vulgare* characters chiefly and few or no *durum* characters; (2) those with *durum* characters chiefly and few or no *vulgare* characters; (3) those with approximately equal numbers of *durum* and *vulgare* characters and a considerable proportion of intermediate ones. The numbers in these groups are 17, 24 and 16, respectively. The proportion in the latter class is extremely small in comparison with the expectation on a basis of free Mendelian assortment. With 13 pairs of characters nearly all plants in a sample of 57 would be expected to fall into this group. In the columns at the right, the striking thing is that the numbers of *vulgare* and *durum* characters are either large or small,—near zero or near 13,—not mostly 6 or 7 as would be expected. In considering the plants with a large number of D or V characters, it is to be remembered that while this number is less than 13, it is usually less only by approximately the number of intermediate characters.

In short, the great majority of the segregates have either *durum* characters chiefly or *vulgare* characters chiefly.

The correlation is brought out more clearly in table 3. The second column gives the number of characters which remain for each plant when the number of its intermediate characters is subtracted from 13 (the

TABLE 2

The condition of the 13 characters in different F_2 plants.

PEDIGREE NUMBER	COMPACTNESS	HEAD FORM	KEEL	MIDDLE TOOTH	LATERAL TOOTH	GLUME SHAPE	KEEL HAIRS	COLLAR	BEARDS	CAVITY OF STEM	DIAMETER OF STEM	SEED HAIRS	SEED FORM	TOTALS				
														V	IV	I	ID	D
F_1	I	I	ID	I	V	I	D	I	IV, I	V, IV	V	V	I	..	..	..	..	..
1–2–2	V	V	V	V	V	V	V	V	V	V	V	V	I	12	..	1	..	..
1–2–3	I	D	I	D	D	D	I	D	IV	D	D	D	D	..	1	3	..	9
1–2–4	D	D	D	V	D	I	D	D	V	D	D	V	D	3	..	1	..	9
1–2–5	V	V	D	D	D	I	V	I	ID	V	V	V	I	6	..	3	1	3
1–2–6	V	V	V	I	D	V	V	I	V	I	V	D	V	8	..	3	.	2
1–2–7	I	I	V	I	D	D	V	V	V	D	D	D	I	4	.	4	..	5
1–2–9	I	D	D	D	D	D	I	D	D	D	D	D	D	..	..	2	..	11
1–2–10	D	D	D	V	D	D	D	D	V	D	D	D	D	2	..	..	.	11
1–2–11	V	I	ID	D	D	I	I	V	ID	IV	V	I	I	3	1	5	2	2
1–2–12	D	D	V	V	D	D	V	D	V	D	D	I	D	4	..	1	..	8
1–2–13	D	D	D	I	D	D	D	V	V	IV	D	V	I	3	1	2	.	7
1–2–14	D	D	ID	V	I	I	I	D	V	IV	V	V	I	4	1	4	1	3
1–2–15	D	D	D	D	D	D	D	D	ID	D	D	I	D	..	..	1	1	11
1–2–16	D	D	I	I	D	D	I	D	D	D	I	D	D	..	..	4	..	9
1–2–17	D	I	I	V	V	V	V	I	V	I	D	I	D	5	..	4	..	4
1–2–18	V	V	V	D	V	I	I	V	ID	V	V	V	V	9	..	2	1	1
1–2–19	D	D	ID	V	D	I	D	D	I	D	D	V	D	2	..	2	1	8
1–2–20	V	V	V	I	V	I	I	V	IV	IV	V	V	V	8	2	3	..	..
1–2–21	I	I	D	D	V	I	D	I	V	I	V	V	D	4	..	5	..	4
1–2–22	V	I	V	V	I	I	V	I	V	V	V	V	V	9	..	4	..	..

TABLE 2 (continued)

PEDIGREE NUMBER	COMPACTNESS	HEAD FORM	KEEL	MIDDLE TOOTH	LATERAL TOOTH	GLUME SHAPE	KEEL HAIRS	COLLAR	BEARDS	CAVITY OF STEM	DIAMETER OF STEM	SEED HAIRS	SEED FORM	TOTALS				
														V	IV	I	ID	D
1–2–23	V	I	I	V	V	I	I	V	IV	V	V	V	I	7	1	5	..	..
1–2–24	D	D	D	D	D	D	D	D	D	I	V	D	D	1	..	1	..	11
1–2–25	I	I	V	V	D	I	V	V	V	IV	V	V	I	7	1	4	..	1
1–2–26	D	D	ID	V	D	D	D	D	V	I	D	D	D	2	..	1	1	9
1–2–27	I	I	ID	I	I	I	I	I	IV	I	V	V	V	3	1	8	1	..
1–2–28	D	D	V	D	I	D	D	D	D	I	D	I	D	1	..	3	..	9
1–2–29	D	D	I	I	I	D	I	I	V	I	D	V	D	2	..	6	..	5
1–2–30	D	D	I	V	I	I	I	I	V	I	D	V	V	4	..	6	..	3
1–2–31	V	I	I	D	V	V	V	V	I	I	V	V	V	8	..	4	..	1
2–1–27	V	V	V	D	D	I	V	V	I	V	V	V	I	8	..	3	..	2
2–1–28	D	I	D	I	D	D	D	I	IV	I	I	V	D	1	1	5	..	6
2–1–29	I	I	I	V	V	V	V	V	V	I	V	V	I	8	..	5	..	..
2–1–31	I	D	V	V	I	V	V	V	V	I	V	V	V	9	..	3	..	1
2–1–32	D	D	I	V	D	I	V	I	I	D	I	V	D	3	..	5	..	5
2–1–33	D	D	D	I	D	D	I	D	ID	D	D	I	D	..	..	3	1	9
2–1–34	I	I	D	I	D	D	I	I	I	I	V	I	D	1	..	8	..	4
2–1–35	V	V	I	D	D	I	V	I	ID	D	D	V	I	4	..	4	1	4
2–1–36	D	D	D	D	D	D	D	V	D	D	D	D	D	1	..	..	..	12
2–1–38	D	D	D	I	I	D	D	D	IV	D	D	V	D	1	1	2	..	9
2–1–39	D	D	ID	V	D	D	I	I	V	I	V	I	I	3	..	5	1	4
2–1–40	V	I	D	I	I	I	V	V	V	V	V	V	V	8	..	4	..	1
2–1–41	D	D	ID	I	D	D	I	D	I	D	D	D	D	..	..	3	1	9

TABLE 2 (continued)

PEDIGREE NUMBER	COMPACTNESS	HEAD FORM	KEEL	MIDDLE TOOTH	LATERAL TOOTH	GLUME SHAPE	KEEL HAIRS	COLLAR	BEARDS	CAVITY OF STEM	DIAMETER OF STEM	SEED HAIRS	SEED FORM	TOTALS				
														V	IV	I	ID	D
23–4–5	I	D	D	V	D	D	D	I	IV	D	D	I	D	1	1	3	..	8
23–4–6	D	D	D	D	D	D	D	D	V	D	I	D	D	1	..	1	..	11
23–4–7	V	V	I	I	V	V	I	V	V	V	V	V	V	10	..	3	..	..
23–4–8	I	D	I	V	V	V	D	I	V	D	V	I	I	5	..	5	..	3
23–4–9	V	I	V	D	V	V	V	D	V	V	V	V	V	10	..	1	..	2
23–4–10	D	D	D	D	D	D	D	D	ID	D	D	I	D	..	..	1	1	11
23–4–11	I	I	I	D	D	D	V	D	IV	I	I	V	V	3	1	5	..	4
23–4–12	V	V	I	V	V	I	V	V	I	IV	V	V	I	8	1	4	..	..
23–4–13	D	D	ID	V	D	D	I	D	V	I	I	D	D	2	..	3	1	7
23–4–14	I	I	V	D	V	V	V	I	I	IV	V	V	V	7	1	4	..	1
23–4–15	D	D	D	V	D	D	D	D	V	D	D	V	D	3	..	..	..	10
23–4–16	D	D	V	I	D	D	V	D	IV	D	D	V	D	3	1	1	..	8
23–4–18	I	I	D	I	V	I	I	V	V	I	V	V	I	5	..	7	..	1
23–4–19	D	D	D	D	D	D	I	I	I	D	D	I	D	..	..	4	..	9
23–4–20	I	D	D	V	D	D	D	D	IV	D	D	V	D	2	1	1	.	9

total number of characters considered). This is, then, the maximum possible number of D characters after the intermediate ones have been removed from consideration. It will be observed that where the possible numbers are high, the actual numbers are either high or low. The middle numbers (4, 5, 6, 7) occur where the possible numbers are smallest. Their absence where high numbers are possible is striking. Similarly, the plants with the smallest actual numbers of D characters do not occur where the possible numbers are smallest.

The lowest line of this table shows the total number of plants for each number of D characters, intermediate conditions being disregarded. The

concentration of the individuals towards the ends of the series is striking. In a typical Mendelian case, the distribution of the numbers would be as in table 4, if no intermediate conditions existed. The chances of getting any plants (out of 57) with few or many *durum* characters are very small. All should have the middle numbers.

TABLE 3

The numbers of plants with the different numbers (0-13) of durum characters.

NUMBER OF INTERMEDIATE CHARACTERS	POSSIBLE NUMBER OF D AND ID CHARACTERS	ACTUAL NUMBER OF D AND ID CHARACTERS													
		13	12	11	10	9	8	7	6	5	4	3	2	1	0
0	13	..	1	1	1	..	..	..	..	..	..	..	..	..	..
1	12	..	2	2	1	2	3	..	..	..	..	..	..	1	1
2	11	..	..	1	..	2	..	1	..	..	..	..	1	..	..
3	10	..	..	..	2	2	1	..	..	..	1	..	2	1	2
4	9	..	..	..	..	2	..	..	..	2	2	..	..	4	2
5	8	..	..	..	..	..	..	..	1	2	3	1	..	..	2
6	7	..	..	..	..	..	..	..	..	1	..	1	..	..	..
7	6	..	..	..	..	..	..	..	..	..	..	..	..	1	..
8	5	..	..	..	..	..	..	..	..	..	1	..	..	..	1
Total		..	3	4	4	8	4	1	1	5	7	2	4	6	8

Table 3 may readily be turned into a similar table for *vulgare* characters, since any character not recorded as I or D is recorded as V.

TABLE 4

NUMBER OF D CHARACTERS	MENDELIAN EXPECTATION FOR 13 CHARACTER PAIRS													
	0	1	2	3	4	5	6	7	8	9	10	11	12	13
Number of plants	1	13	78	286	715	1287	1716	1716	1287	715	286	78	13	1

Since this correlation exists with respect to the whole 13 characters, naturally each pair of *durum* or *vulgare* characters shows correlation. For those characters which can be accurately measured, the coefficient of correlation is as follows:

Compactness and head form 0.524 ± 0.054
Compactness and diameter of stem 0.220 ± 0.052
Compactness and beard length 0.096 ± 0.054

Some pairs of characters tend to be associated much more strongly than others. In general, these are the ones which are always or nearly always characteristic of the species. Thus, *durum* compactness and head form are more strongly correlated than either is with long beards. The former two characters distinguish nearly all *durum* varieties from nearly all *vulgare* varieties. On the other hand, though nearly all *durum* varieties have long beards, *vulgare* varieties may have either long or short ones. The more definitely a quality is characteristic of *durum* wheat, the more difficult it is to get it in association with *vulgare* characters.

In no case, however, is the correlation complete. Hybrid lines have been established, for example, even with the *vulgare* looseness and the *durum* ratio of width to thickness. It should therefore not be impossible to break the correlation for any desired character. In actual breeding practice it will not be necessary to get any single *durum* character away from all the others.

Behavior of intermediate segregates

The breeding behavior of those F_2 plants which are intermediate (i.e., which have a high proportion of intermediate characters and approximately equal numbers of *durum* and *vulgare* characters) is characteristic. In the first place they showed a high degree of sterility. Three of the 16 plants produced no offspring at all, and the average number of offspring for the whole 16 was 4.1. The *durum*-like and *vulgare*-like segregates were much more fertile. Though never more than 16 seeds of each plant were sown, the average number of offspring to reach maturity was 9.7. Nevertheless, a considerable number of *durum* and *vulgare*-like segregates did show partial sterility and some of their offspring died before reaching maturity.

In the second place, the offspring of the intermediate plants were generally not intermediate but either *durum*-like or *vulgare*-like. The F_2 plants segregated in the same way as F_1. For example, the offspring of 1-2-29 and 23-4-8 showed a distribution of characters as given in table 5. Thus, combinations of approximately equal numbers of *durum* and *vulgare* characters are not perpetuated in many offspring in later generations. And since these intermediate F_2 plants are relatively few in number and sterile in addition to showing this segregation, a larger and larger proportion of the segregates become *durum*- or *vulgare*-like. On the other hand, plants with a combination of chiefly *durum* characters with a few *vulgare* ones, or *vice versa*, may breed true.

CHROMOSOME NUMBERS IN RELATION TO PLANT CHARACTERS

KIHARA (1919, 1921) and SAX (1922) have shown that in *durum* wheats the haploid chromosome number is 14, while in *vulgare* it is 21 and in einkorn 7. In F_1 hybrids between *durum* and *vulgare* the heterotypic plate shows 14 bivalents and 7 univalents. At the homotypic division,

TABLE 5

Characters of the offspring of intermediate F_2 plants.

PEDIGREE NUMBER	CHARACTERS		
	V	I	D
1–2–29–1	11	1	1
1–2–29–2	1	3	9
1–2–29–3	2		11
1–2–29–4	3	2	8
23–4–8–1	10	1	2
23–4–8–2	3	2	8
23–4–8–3	3	6	4

the 7 univalents do not divide, but are distributed at random to either pole. SAX found that the great majority of F_3 plants had either 14 or 21 chromosomes. The 14-chromosome plants were of the *durum* type and the 21-chromosome plants were *vulgare*-like. To account for these results and others, including sterility, he assumes that gametes with 17 and 18 chromosomes do not develop, and that the nearer the chromosome number approaches the parental conditions (14 and 21) the more likely is the gamete to function properly. Most of the offspring will therefore result from the meeting of gametes with 14 or 21 chromosomes.

During the past summer the chromosomes of a considerable number of F_2 plants were studied by the BELLING (1921) method, and these plants have since been examined with respect to the thirteen characters used in this paper. SAX's counts in a similar cross were made in F_3 plants. It was considered desirable to secure information in regard to F_2 conditions, because many of the F_2 possibilities are eliminated through sterility and correlation. It would be very difficult from F_3 plants alone to judge accurately the conditions in a representative F_2 generation, and therefore to estimate the processes which produced them.

Satisfactory counts were obtained in 41 plants, in many cases at both heterotypic and homotypic division. In some other cases in which accurate counts were made, the plants later proved sterile, so that the seed characters could not be studied, and these have not been included in the results. In nearly every case these counts were 16 to 19. Since it is desirable to

raise F_3 plants in order to check carefully the F_2 classification of characters, the detailed description of the results is reserved until that generation has been raised, and the results are therefore given only in summary here.

A much larger proportion of plants with chromosome numbers from 16 to 19 were found than SAX (1922) records for F_3 plants. The varieties used may behave differently or the 50 F_3 plants used by him may not give an average representation of the F_2 generation. But the difference is presumably due chiefly to the high degree of sterility of these plants and gametic elimination. If there were no elimination of gametes and no selective fertilization, only 2 F_2 segregates out of about 6000 should have 14 or 21 chromosomes. But even if only 14- and 21-chromosome gametes function, there should be at least twice as many plants with intermediate numbers as with 14 or 21. It is quite possible that the elimination of female gametes is not so extensive as that of males, since there is only one for each ovule and no competition.

Table 6 shows the distribution of the plants with respect to the number of chromosomes and number of *durum* characters (out of a possible 13). Nearly all the plants in the group with chromosome number "14, 15" really had 14. In a few cases it could be stated with certainty that the number was not greater than 15, but it could not be stated definitely whether it was 14 or 15. Similarly, nearly all those in the group "20, 21" really had 21. And most of those in the group "16 to 19" really had 17 or 18.

TABLE 6

Chromosome number and plant characters.

CHROMOSOME NUMBER	NUMBER OF *durum* CHARACTERS													
	0	1	2	3	4	5	6	7	8	9	10	11	12	13
14, 15	..	1	..	..	..	..	..	..	3	7	4	1	..	..
16 to 19	1	..	3	1	2	2	3	1	2	1	..	..	..	..
20, 21	2	4	2	..	1	..	..	..	..	..	..	..	..	..

It will be seen that nearly all the plants with 14 or 15 chromosomes had a large number of *durum* characters, while those with 20 or 21 had none or few. It is probable that the single record of one *durum* character in the "14, 15" group is due to an error in records. In those plants with 16 to 19 chromosomes, the number of *durum* characters is for the most part intermediate. A few plants in this group were chiefly *durum*. Some of the 14-chromosome plants lacked one or a few of the most characteristic *durum* features, such as compactness, keel, or head type. And some of the 21-chromosome plants had one or a few of these *durum* characters.

Table 7 shows the distribution of the *vulgare* characters in the same way. Nearly all the 14-chromosome segregates had few *vulgare* characters, while those with 21 chromosomes had many. But there is no unbroken association of any one *vulgare* character with the 21-chromosome condition. The plants with a large number of intermediate characters generally had 16 to 19 chromosomes. On the whole there is a much less settled chromosome condition with numbers 14 and 21 than is reported for F_3 plants and, correspondingly, a much greater variety of character combinations.

TABLE 7

Chromosome number and plant characters.

CHROMOSOME NUMBER	NUMBER OF *vulgare* CHARACTERS													
	0	1	2	3	4	5	6	7	8	9	10	11	12	13
14, 15	..	3	8	3	1	..	..	..	..	1	..	..	..	..
16 to 19	..	1	2	4	4	2	2	..	1	..	..	..	..	..
20, 21	..	..	..	..	..	..	1	..	1	2	2	2	1	..

It is also evident that the number of 21-chromosome plants and of *vulgare*-like segregates is less than the number of 14-chromosome and *durum*-like segregates. This has been frequently observed in other experiments.

RUST-RESISTANCE IN RELATION TO OTHER CHARACTERS

The *durum* parent (Iumillo) of this cross is very resistant to stem rust. The pure line which has been used is highly resistant to all the biologic forms which have been found in Western Canada by NEWTON (1922). A brief summary follows of my data on the inheritance of resistance in this cross and the correlation of resistance with other characters.

All records given are from plants artificially inoculated in the greenhouse with a single biologic form of stem rust. This is number XVII of STAKMAN and LEVINE (1922), and is one of the most serious in Western Canada. The rust was supplied from time to time by W. P. FRASER of the DOMINION LABORATORY OF PLANT PATHOLOGY, situated at this University. In the earlier inoculations, F_2 plants were used and any which showed resistance were tested at least twice. Their F_3 offspring were also tested and the F_2 classification confirmed or corrected. Since greenhouse conditions during winter in Western Canada are very unfavorable for wheat because of lack of light, many plants were lost or proved sterile. The F_2 tests were therefore abandoned after a time, and only F_3 plants used, so that no promising line might be lost. When all or most of the plants of a small F_3 family proved susceptible, the F_2 parent was classified as

susceptible. Since a few F_2 plants are sterile even under field conditions, no information concerning these was secured when F_3 plants only were used, and the ratios would be inaccurate to that extent. Plants were classified as resistant when they showed no uredinia at all or small, isolated ones surrounded by hypersensitive areas. These would come under types 0, 1 or 2 of STAKMAN and LEVINE (1922). All other plants were classified as susceptible.

Tests with both F_2 and F_3 plants

Total F_2 plants tested	876
Susceptible in F_2 test	771
Resistant or escaped in F_2 test	105
Sterile or dead after F_2 test	35
Susceptible families in F_3 test	18
Final resistant	52

If the sterile and dead F_2 plants are classified with the resistant plants, the ratio of susceptible to resistant is 789:87 or 9.0:1. If they are classified with the susceptible plants, the ratio is 824:52 or 15.8:1. Since sterile plants are generally weaklings and since rust does not develop well on weak plants, they should probably be classified chiefly with the susceptible ones. In any case it is evident that there is no simple Mendelian ratio.

Tests with F_3 plants only

Total number of families tested	2256
Susceptible families	2097
Resistant families	159

Ratio, susceptible : resistant, 13.2 : 1.

HAYES (1920) has reported finding a ratio of 1030 susceptible to 106 resistant or 9.7:1. His figures, however, include the results with two sets of hybrids, Marquis×Kubanka and Marquis×Iumillo. The factorial conditions in the two *durum* races may not be the same, since they behave differently to certain rust strains.

Characters of resistant segregates

Altogether, in this experiment 211 F_2 plants or F_3 families proved resistant. Of these only 3 possessed chiefly *vulgare* characters, all the others being clearly of the *durum* type. The three *vulgare*-like plants are not as resistant as the *durum* parent, but are much more resistant than the *vulgare* parent. HAYES reports obtaining 2 *vulgare*-like plants in his 106 resistant segregates. According to my observation of their behavior

in Western Canada, HAYES's hybrids also are not so resistant as their *durum* parent.

There is thus evidently a very high degree of correlation between rust-resistance and *durum* characters. This is a particular example of the general correlation of all *durum* characters in this cross. The fact that rust-resistance depends on more than one factor, as shown by the breeding results, makes the correlation more pronounced than in other cases. It is more difficult to get the two or more factors for rust-resistance in the same segregate without taking with them many other *durum* characters, than it would be to get a single factor for resistance free from other *durum* characters.

Some *vulgare* characters are found in resistant segregates much more commonly than others. Thus the *vulgare* laxity and type of head are rarely found in resistant segregates while the keel, length of beards, or seed hairs of resistant plants are frequently of the *vulgare* type.

DISCUSSION

SAX concludes that the correlation of characters as well as the partial sterility is due to the behavior of the extra 7 chromosomes of *vulgare* wheat. The addition to the number 14 of any number less than a complete set of 7 results in an unbalanced condition which kills or greatly handicaps the gametes. Therefore gametes with 14 and 21 chromosomes are the ones which function chiefly. This is supported by his finding that the great majority of F_3 plants studied have a haploid number of either 14 or 21. It should be pointed out, however, that even if all gametes have either 14 or 21 chromosomes, there should be at least as many F_2 plants with an intermediate chromosome number as with 14 and 21. Therefore either the F_2 plants with an intermediate number are sterile or they produce F_3 plants with 14 and 21 only.

Since the 14-chromosome segregates are *durum*-like and the 21-chromosome segregates are *vulgare*-like, it follows from this conception that the *vulgare* characters are due to the extra 7 *vulgare* chromosomes. Fourteen of the *vulgare* chromosomes must be practically the same as fourteen *durum* ones. They mate regularly with them and are interchangeable. According to this view, even if all the 14 chromosomes of an F_2 plant came from the *vulgare* parent, it would still be a *durum*. Then the extra 7 chromosomes must always be the same ones and so unlike any of the *durum* ones, that they rarely mate with them.

But there are several kinds of evidence which seem to be opposed to the conception that the *vulgare* genes are carried only in the extra seven

chromosomes, and to the inferences which may be drawn from that conception: (1) Segregates are obtained which are *durum*-like in all but one or a few features, and these features may be the most characteristic of *vulgare*. Similarly, segregates are obtained which are *vulgare*-like in all but one or a few characters. (2) Long-established varieties of wheat are known which present similar combinations. For example, a few races of *durum* wheat are known, which have the *vulgare* hollow stem; others have mealy endosperm, others lax heads, others are beardless. Similarly, some long-established *vulgare* varieties have certain *durum* characters, such as fully-keeled glumes, solid stems, compact heads. (3) It has been shown above that 14-chromosome segregates may actually have some *vulgare* features, even the most characteristic ones, and that 21-chromosome segregates may actually have some characteristic *durum* features. (4) There must really be great differences between the primary 14 chromosomes of *vulgare* and those of *durum*, because several characters quite absent from both appear in some F_2 plants, even the striking adherence of the glumes to the kernel, which is characteristic of emmer wheats. (5) Characters which distinguish *vulgare* from *durum* wheats are commonly present in other 14-chromosome wheats, so that they can not be due to the extra 7 chromosomes. Thus, *T. polonicum* is commonly lax-headed like *vulgare*; *T. turgidum* has the short inflated glumes of *vulgare*; *T. dicoccum* has the brush of hair on the seed. (6) *T. monococcum*, the only species with the primary number 7, has several characters present in *vulgare* but not in *durum*, such as hollow stem, brush of seed hairs, short glumes. It is difficult to see how these characters, which are present in a wheat with 7 chromosomes, absent from one with 14, and present again in one with 21, can be due to duplication of genes, or why they should be present only in the particular 7 extra chromosomes of *vulgare* wheat. (7) There are great variations in the degree of sterility in crosses between different 14-chromosome wheats and *vulgare* wheats. Therefore, it is probably not due to the extra seven chromosomes only.

Owing to these difficulties, one is inclined to view favorably another possibility, namely, the effect of incompatibilities amongst the chromosomes. In this conception, the differences between the *durum* and *vulgare* chromosomes, which must be very great, exist in many or all of them, and not merely in the extra 7. The 14 *durum* chromosomes or the 21 *vulgare* chromosomes work together properly, but the differences between them are so great that combinations of the two sorts may be incompatible. A viable, properly functioning condition may result only when the chromosomes are mostly from the *durum* parent or mostly from the *vulgare* parent.

Then the characters also would be all or chiefly *durum*, or all or chiefly *vulgare*. The substitution of one or a few chromosomes of one species in a set of the other species might not be too disturbing for proper functioning. Thus, the common occurrence of one or a few characters of one species in a segregate of the other type would be accounted for. The other points mentioned in the last paragraph also support this view.

Additional points supporting this conception are: (1) A considerable proportion of the seeds on F_1 plants produce offspring which fail to grow properly to maturity. Therefore, though the gametes form and function, nevertheless the combinations which they produce cannot function properly in the zygote. There would appear to be incompatibilities in the vegetative tissues. (2) A good many plants in F_2 and F_3, which examination shows to have only 14 chromosomes, are weak and partially sterile. In these there can be no effect of an unbalanced chromosome number. Their weakness and sterility are apparently due to chromosome incompatibilities.

It is to be expected that the behavior of these long-established species of wheat should be unlike that of forms in which the chromosome differences are of recent or experimental origin. The species of wheat have been in existence so long (since prehistoric times) that many changes in chromosome constitution must have taken place since the original changes in chromosome number. In recent examples of polyploidy the extra chromosomes presumably carry the same genes as the others, so that any differences in characters are due only to duplications and numerical relationships.

Whatever our interpretation of the causes of the correlation may be, the results show that it is not absolute, that we do get *durum*-characters in segregates which are otherwise *vulgare*-like. Even the most characteristic of the *durum* qualities may be found in plants all of whose other characters are *vulgare*. In agreement with this we find 14-chromosome plants with odd *vulgare* characters and 21-chromosome plants with odd *durum* characters. It therefore appears to be premature to conclude that it will be impossible to get any desirable *durum* character in combination with *vulgare* characters in a wheat of *economic* importance.

The difficulties with respect to rust-resistance seem to be greater than with respect to other *durum* characters. This may be due to the fact, as seen from the results, that resistance depends on more than one factor and to carry all over into a *vulgare* type may also involve carrying over other *durum* characters. But rust-resistant *vulgare*-like segregates have actually been secured both by HAYES and by the writer, and have maintained their

resistance at many different stations (FRASER 1923). It is true that these are not so resistant as the *durum* parent. Probably not all the factors have yet been carried over into the *vulgare* type, or they may not function so effectively in a set of chromosomes which are mainly *vulgare*. Whether they are sufficiently resistant for practical purposes remains to be seen.

SUMMARY

1. Thirteen pairs of characters which distinguish *Triticum durum* from *T. vulgare* were studied in F_2 and F_3 plants. The condition of each plant (*vulgare*, *durum* or intermediate) with respect to each of them is recorded.

2. The F_2 segregates may be divided into 3 groups: (1) those with *durum* characters only or chiefly; (2) those with *vulgare* characters only or chiefly; (3) those with a considerable number of intermediate characters and approximately equal numbers of *durum* and *vulgare* characters.

3. The *durum*-like segregates commonly showed one or a few *vulgare* features, sometimes even the most characteristic ones. Similarly, the *vulgare*-like segregates commonly showed one or a few *durum* features.

4. The intermediate plants showed a high degree of sterility and produced a high proportion of *durum* and *vulgare* types in F_3. Intermediate types thus tend to disappear in the third and later generations.

5. Chromosome numbers and their relation to the 13 characters is recorded for F_2 plants. A much larger proportion of plants showed chromosome numbers intermediate between those of the parents (14 and 21) than is reported for F_3 plants. The 14-chromosome plants were of the *durum* type and the 21-chromosome plants were of the *vulgare* type, but most plants of each type showed a few characters of the other type, even the most characteristic ones.

6. Results are given concerning the inheritance of rust-resistance in this cross. Records are available for more than 3000 F_2 plants and F_3 families (about 30,000 plants in all) and these show the F_2 ratio of susceptible to resistant to be about 13:1. Of the resistant plants, very few were of the general *vulgare* type, though numerous resistant plants contained a few *vulgare* characters. The few resistant *vulgare*-like plants were not so resistant as the *durum* parent. The correlation of rust-resistance and *durum* characters has been broken, but, owing to the fact that it depends on more than one factor, it may be very difficult to get the full *durum* resistance in *vulgare* types without other *durum* characters.

7. Evidence is brought forward which is considered to indicate that the correlation of characters and partial sterility depends, in part at least, on chromosome incompatibilities, and not entirely on the elimina-

tion, due to unbalance, of gametes with intermediate chromosome numbers.

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